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AYK – Ecotypic Variation in AYK Sockeye Stocks

by:

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I. ABSTRACT:

We investigated the degree of ecotypic (morphological and life history), genetic, and habitat diversity associated with sockeye salmon spawning populations in two drainages (the Holitna River and Telaquana Lake/Stony River) in the Kuskokwim River basin. Telaquana populations showed greater morphological, size, and age diversity than did Holitna populations, which were older, larger, and showed less variation in male morphology. Female size and its correlate, egg size, showed little variation among sites and within drainages, likely due to the relative lack of variation in sediment size on the spawning grounds. The two drainages had comparable levels of genetic (allelic) diversity; however Telaquana populations showed greater genetic structure and lower heterozygosity, consistent with less gene flow, than did Holitna populations. Genetic structure was greater than that observed at the same loci in Bristol Bay; we hypothesize that one cause of this difference in the presence of at least two different ancestral lineages within the Kuskokwim River. When compared to Bristol Bay populations, Holitna sockeye showed decreased ecotypic diversity, but Telaquana populations had a level of ecotypic diversity comparable to that of Bristol Bay. We attributed this finding to the relative dearth of spawning habitat types (biotopes) available in the Holitna River (riverine), while Telaquana supported spawning biotope complexity similar to that found in Bristol Bay (riverine, beach, and inlet creek habitats). The findings of our study predict that the 'portfolio effect' will apply to Telaquana Lake, with ecotypic diversity contributing to run stability at the drainage level, whereas Holitna returns would be expected to show greater inter-annual fluctuations due to decreased ecotypic diversity. Long-term support of escapement monitoring on both systems will be required to test this prediction.

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III. INTRODUCTION:

The overall goal of this study was to quantify the biocomplexity contained within two sockeye salmon stocks in the Kuskokwim River drainage. In the context of salmon fisheries, "biocomplexity" describes the degree to which regional stocks are subdivided into locally adapted populations that differ from neighboring populations in life history and morphological traits. When assessed at the regional scale, this diversity (described as 'ecotypic' due to the importance of environment in affecting these traits) is increasingly recognized as an important component of the biology and management of fisheries around the globe (Hilborn et al. 2003, Schindler et al. 2010).

Biocomplexity/ecotypic diversity is particularly relevant to Pacific salmon, in which genetic, life history, and morphological diversity are structured hierarchically. Groupings can be identified at the species range scale (e.g., regions delineated by common ancestry via recolonization from glacial refugia; Bernatchez and Wilson 1998), the regional scale (e.g., stocks, or aggregations of populations defined by biological and/or management criteria; Ricker 1972, Mundy and Mathiesen 1981), the local spawning population or deme scale (Policansky and Magnuson 1998), or even at a fine local scale (specific sites within spawning localities; Quinn et al. 1999). Variation at these hierarchical levels results from processes acting at different spatial and temporal scales, including paleohistory (glaciation), climate regime shifts over century and decadal time scales (Mantua et al. 1997, Beamish et al. 1999), and the interaction between local environmental conditions and population genetic history (Hutchings 2003). These processes, acting over multiple spatial and temporal scales, cause great difficulty for fishermen, managers, and fisheries biologists seeking to understand the causes and consequences of fluctuations in salmon abundances (McPhee et al. 2009a). Yet accumulating evidence suggests that this very complexity may be an essential component of regional fishery stability over time.

The best-known example of the connection between ecotypic diversity and fishery stability comes from the sockeye salmon (*Oncorhynchus nerka*) fishery of Bristol Bay, Alaska. Due to the diversity of spawning habitats available in this region and the different natural and sexual selective pressures imposed by these different environments, coupled with strong spawning site philopatry, sockeye salmon show remarkable, site-specific variation in a number of traits, including spawning morphology, timing of life history, and egg size (reviewed in Quinn 2005). Because of these population-specific differences, each individual spawning population appears to respond differently to environmental change imposed by ocean conditions, regional and local weather patterns, and fishing pressure. Yet, because of the high diversity in population characteristics and attendant responses to environmental factors, population size at the regional (aggregated-stock) scale remains relatively constant (Hilborn et al. 2003, Schindler 2010). This constancy at the regional scale allows for a relatively predictable, resilient fishery. However, maintaining this resilience means conserving the local components of this complexity, such that weak stocks cannot be ignored today because they might become the strong stocks of tomorrow (Hilborn et al. 2003).

Subsistence and commercial fishermen of the Arctic-Yukon-Kuskokwim (AYK) region have not enjoyed the stable (and often lucrative) conditions experienced in the Bristol Bay region. Communities in the AYK region experienced economic hardship when salmon stocks inexplicably crashed during the period of 1997-2002 (AYK SSI 2006). The AYK region is vast, remote, and does not have the resources to support the kind of research effort that has been conducted in Bristol Bay. Thus an important question regarding the future of AYK fisheries, which our proposal seeks to address, is how can we apply the lessons about biocomplexity learned in Bristol Bay to the AYK region?

The first step in making the link between biocomplexity in Bristol Bay versus that of AYK is quantifying the amount ecotypic diversity in AYK salmon stocks and determining whether this diversity is arrayed over space at a scale comparable to that of Bristol Bay. It cannot be assumed that AYK salmon stocks are structured the same way as in Bristol Bay. An obvious difference is that fisheries in the AYK region have traditionally been focused on chum and Chinook salmon (*O. keta* and *O. tshawytscha*, respectively), and

ecotypic variation is not as well characterized in these species (but see Gilk et al. 2007). Sockeye salmon returns to the Kuskokwim River have increased dramatically since 2003 (Linderman and Bergstrom 2009), suggesting that lessons learned from the Bristol Bay sockeye fishery are increasingly relevant to the AYK region as this fishery gains importance.

Stony River/Telaquana Lake has always been considered the major sockeye salmon producer in the Kuskokwim due to the presence of sockeye-rearing lakes at its headwaters. However, results of a recent radiotelemetry study found that the majority of sockeye in the Kuskokwim appear to be headed to the upper Holitna River (S. Gilk, ADFG, pers. comm.). In contrast to the lake-type sockeye predominant in Bristol Bay, these Holitna sockeye are thought to be river-type due to the lack of suitable lake rearing habitat in the Holitna system (Molyneaux and Brannian 2006). River-type sockeye juveniles forego rearing in lake habitats to rear instead in rivers or migrate directly to sea (Wood 1995, 2007).

River-type sockeye often possess greater genetic diversity and show less population structure over space compared to lake-type sockeye, where the nursery lake appears to be the fundamental unit of genetic population structure (Wood 1995, Gustafson and Winans 1999, Beacham et al. 2004). These differences in genetic structure clearly have implications for the way ecotypic variation is expected to be distributed over space, suggesting that river-type sockeye salmon in the Kuskowkim should be more homogeneous than Bristol Bay lake-type sockeye. Yet, our recent study of river-type sockeye salmon in the Kwethluk River, a tributary of the lower Kuskokwim with ca. 4,000 adults returning annually based on weir counts, found strong genetic structure over small geographic distances (McPhee et al. 2009b) suggesting that the potential for ecotypic differentiation in Kuskokwim sockeye is high. It is imperative to better understand the population structure of these Kuskokwim sockeye, both in terms of genetic and life history/morphological diversity, as all signs point towards sockeye becoming a more important component of local fisheries in the future. Furthermore, as these populations continue to expand in the AYK region it will be important to quantify how they change over time, particularly in life-history traits such as spawning timing that contribute to reproductive isolation and genetic stock structure (Varnavskaya et al. 1994, Quinn et al. 2000).

The motivation of this study was to determine to what extent we can apply the lessons about biocomplexity learned in Bristol Bay to sockeye in the Kuskokwim region. To that end, we quantified genetic and ecotypic (life-history, morphological) diversity in two sockeye systems within the Kuskokwim drainage: upper Holitna River and Stony River/Telaquana Lake (from hereon, referred to as 'Holitna' and 'Telaquana', respectively). We related this population diversity to habitat complexity. Finally, we compared diversity found in the Kuskokwim to diversity previously quantified in Bristol Bay. How ecotypic and genetic diversity is arrayed in the Kuskokwim compared to that of Bristol Bay has implications for expected future stability of sockeye returns in the Kuskokwim.

IV. OBJECTIVES:

The overall purpose of the study was to quantify biocomplexity (the spatial scale of genetic and ecotypic diversity) in sockeye salmon in the Kuskokwim drainage. This was accomplished with intensive field studies of sockeye salmon in the Holitna and Telaquana drainages and by comparing our results to existing data from Bristol Bay sockeye populations. Specifically, our objectives were:

1) To characterize ecotypic and neutral genetic diversity within and between sockeye spawning populations in the Holitna and Telaquana drainages;

2) To identify physical features of spawning habitat and to quantify environmental complexity within and between sockeye spawning locations in the in the Holitna and Telaquana drainages;

3) To compare ecotypic and genetic differentiation as a function of geographic distance and environmental complexity in the Kuskowkim drainage and Bristol Bay systems.

For the most part, our objectives were met. We were able to quantify genetic and ecotypic diversity in sockeye salmon from multiple localities (including different spawning biotopes, or habitat types) in both Holitna and Telaquana drainages. We were also able to compare morphological and genetic diversity from these Kuskokwim localities to those from Wood River and Iliamna lakes in Bristol Bay. The third objective was met to a lesser extent. Because our GIS personnel at Flathead Lake Biological Station (FLBS) were committed to another grant at the same time, we were unable to use them to the extent originally planned. Second, the spatial scale of sockeye salmon spawning habitats was much smaller than the scale of analysis of FLBS's Riverscape Analysis Project (RAP), and much of the habitat in Telaquana and Bristol Bay was lacustrine, which was not readily analyzed within the RAP framework. As such, the spatially-explicit component of the analysis was not met to the extent originally proposed. However, we were still able to quantify habitat diversity within and among localities within our study areas, and to examine how sockeye salmon morphology varied with habitat features in both the Kuskokwim and Bristol Bay.

V. METHODS:

Study area

This study took place at two regions within the Kuskokwim River basin of western Alaska: the Holitna River and Telaquana Lake, which drains into the Stony River (Figure 1). The Holitna River is a large river system, comprised mainly of large meanders in its lower stretch but opening up into a series of active floodplains further up in the drainage, with dynamic channel migration and interaction of the river channel with riparian and hyporheic zones. Sockeye are found spawning within parafluvial springbrooks and side channels throughout the upper portion of the drainage. Telaquana Lake is a glacially-carved lake situated within Lake Clark National Park that drains into the Stony River of the Kuskokwim. Sockeye salmon are found spawning in Telaquana River (the outlet), several beaches within the lake, and in inlet creeks at the head of the lake. Inlet creeks erupt from hyporheic flow at the head of the lake, and many are influenced by beaver dam activity.

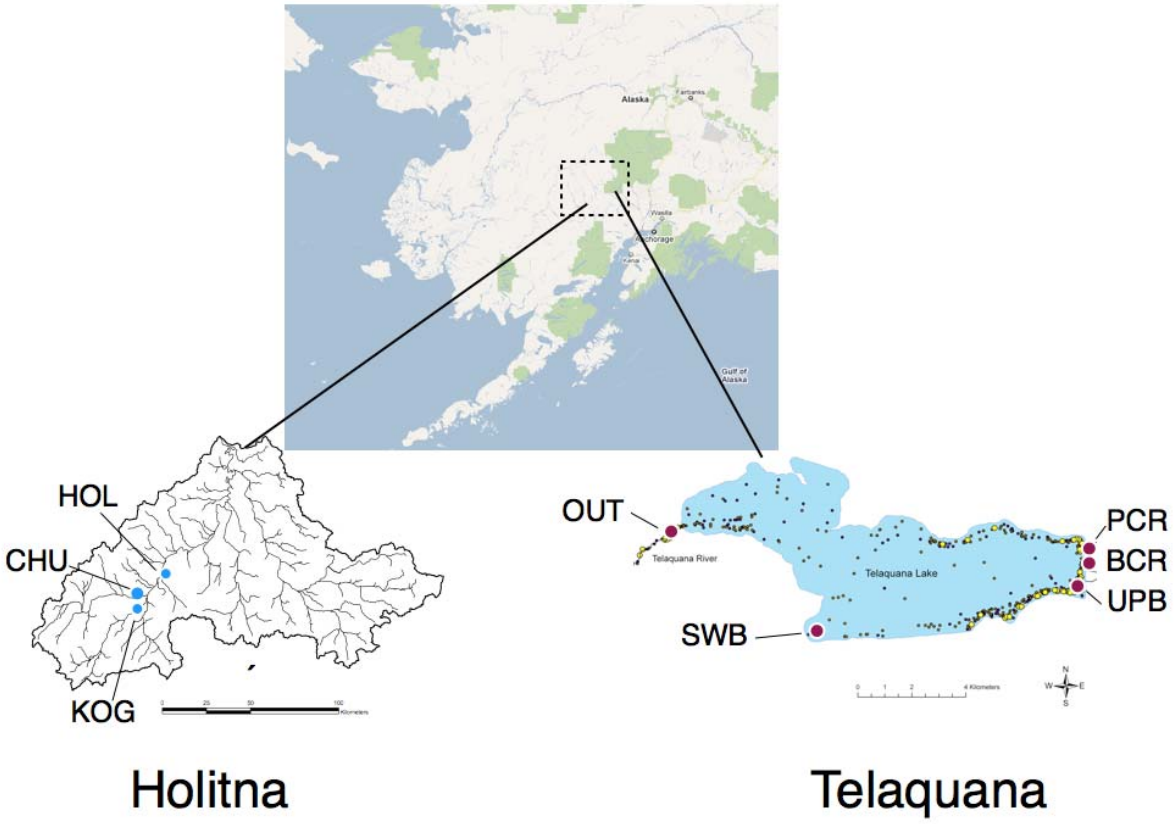

Figure 1. Study area.

Fish and habitat sampling

From 4 – 15 Aug 2008, we sampled adult sockeye salmon on the spawning grounds in three locations within the Holitna drainage: Kogrukluk River ('KOG', UTM Zone 4 559701 E 6740187 N), Chukowan River ('CHU', UTM Zone 4 556874 E 6745584 N), and the mainstem of the Holitna River ('HOL', UTM Zone 4 556874 E 6745584 N). From 29 Aug – 3 Sep 2009, we sampled adult sockeye salmon from spawning grounds in five locations within Telaquana Lake: Telaquana River which forms the outlet of the lake ('OUT', UTM Zone 5 444139 E 6759213 N), two unnamed inlet creeks at the head of the lake ('BCR', UTM Zone 5 459270 E 6757919 N, and 'PCR', UTM Zone 5 459174 E 6758105 N), and lakeshore spawning areas at the head of the lake ('UPB', UTM Zone 5 459230 E 6756829 N) and in the SW corner of the lake ('SWB', UTM Zone 5 449147 E 6755089 N). Personnel and organizations involved in fish and habitat sampling were in 2008, Dave Cannon (Kuskowkim Aquatics Consulting), Glen Lindsey (Kuskokwim Native Association college intern), and Megan McPhee (at the time, FLBS; now UAF), and in 2009, Dan Young, Jerry Mills, and Jeannette Mills (National Park Service), and Megan McPhee (at the time, FLBS; now UAF).

Adult sockeye salmon were collected by seine and held in creek or lake water prior to individual handling (body measurement, photographs, and DNA and egg sample collection). Individuals were anesthetized in clove oil (Woody et al. 2002) and measured for total length (TL), mid-eye to hypural length (MEHP), and body depth (BD) following Blair et al. (1993). The left side of each fish, placed on a flat surface, was photographed using a Nikon D40 digital camera on a tripod. A level was used to ensure that the camera was pointing straight down at the fish, and at least two images were captured per individual. We took a

small piece (~ 10 mm^2) of rayed-fin tissue from each individual and stored it in 95% ethanol for subsequent genotyping; this fin clip also served as a mark to prevent duplicate sampling of recaptured individuals. From females, we sampled ~ 50 eggs per individual and fixed these in 10% formalin for subsequent egg diameter measurement. Fishes were allowed to recover from anesthesia and then released back to the spawning grounds.

Habitat at each of the fish sampling grounds was characterized by temperature, conductivity, vertical hydraulic gradient (degree of up/down-welling), depth, sediment size, and discharge. At each site we collected 8 point measurements of water temperature, conductivity (using a YSI© EC300 handheld conductivity meter), depth, and current velocity both within redds and in non-redd sites selected haphazardly within the sampling area. We also used a minipiezometer to measured vertical hydraulic gradient (VHG) at 16 haphazardly chosen point following the Method 3 of Dahm et al. (2007), except that we did not require an outer casing for driving the minipiezometer into the substrate. For measuring VHG at redds, we installed the minipiezometer just downstream of redds to avoid disturbing developing eggs. Substrate was characterized in two ways. First, we estimated the proportion of substrate surface area that consisted of fine sediments in areas not disturbed by spawning activity, in order to characterize cover by fines prior to spawning. Second, we estimated the size distribution of particles larger than fine sediment using pebble counts (Kondolf and Li 1992). At Telaquana sites, where water quality permitted, we also took digital photos of substrate to estimate the distribution of substrate particle sizes (via digitizing the length of the largest axis of particles). Velocity was measured at 8 haphazardly selected sites per locality, using a Rickly Hydrological pygmy current meter at Holitna sites and a Marsh-McBirney Flo-Mate meter at Telaquana.

Toward the end of the spawning season (16 – 19 Aug 2008 for Holitna and 6 Sep – 21 Oct 2009 for Telaquana), we collected otoliths from spawned-out carcasses. We identified sex and length (mid-eye to hypural) for each otolith collection. Otoliths were sent to Dr. Craig Stafford (University of Montana) for aging (number of years in freshwater and number in saltwater). Due to the delayed spawning season in 2008 we were unable to collect otoliths at each of our sampling sites; otoliths were thus collected opportunistically at Kogrukluk weir in addition to our sampling site on the Chukowan River (CHU). In 2009, high bear predation in the inlet tributaries and beach localities precluded adequate collections from each of our sampling sites; samples were pooled for upper localities (PCR, BCR, and SWB) as we could not assign a carcass back to a spawning locality with confidence. We obtained adequate otolith samples from the outlet (OUT) site. Individual fish ages (estimated by number of fresh- and saltwater growth increments) were plotted against body size (MEHP) to estimate the age distribution of spawning sockeye salmon from each drainage; testing for differences in size-at-age among spawning sites within each drainage was not possible.

Morphometric diversity

Geometric morphometric analysis was restricted to males, as they are subject to the greatest amount of sexual and natural selection on body shape (Blair et al. 1993, Gende et al. 2004). Of the two digital images taken per fish, we chose the better image based on visual inspection. Only images that captured the entire body, showed no evidence of body flexion, and included a readable measuring tape or calipers were digitized. We placed 17 landmarks (Figure 2) on digital images using tpsDIG2 (F. J. Rohlf, life.bio.sunysb.edu/morph/). The same individual did all of the digitization, and the order of digitization was random with respect to sampling locality. Landmarks were scaled to absolute size by digitizing the millimeter bar (from tape measure or calipers) included in the digital photograph. Landmark data were imported into MorphoJ v 1.02h (Klingenberg 2011) for all subsequent geometric morphometric analyses.

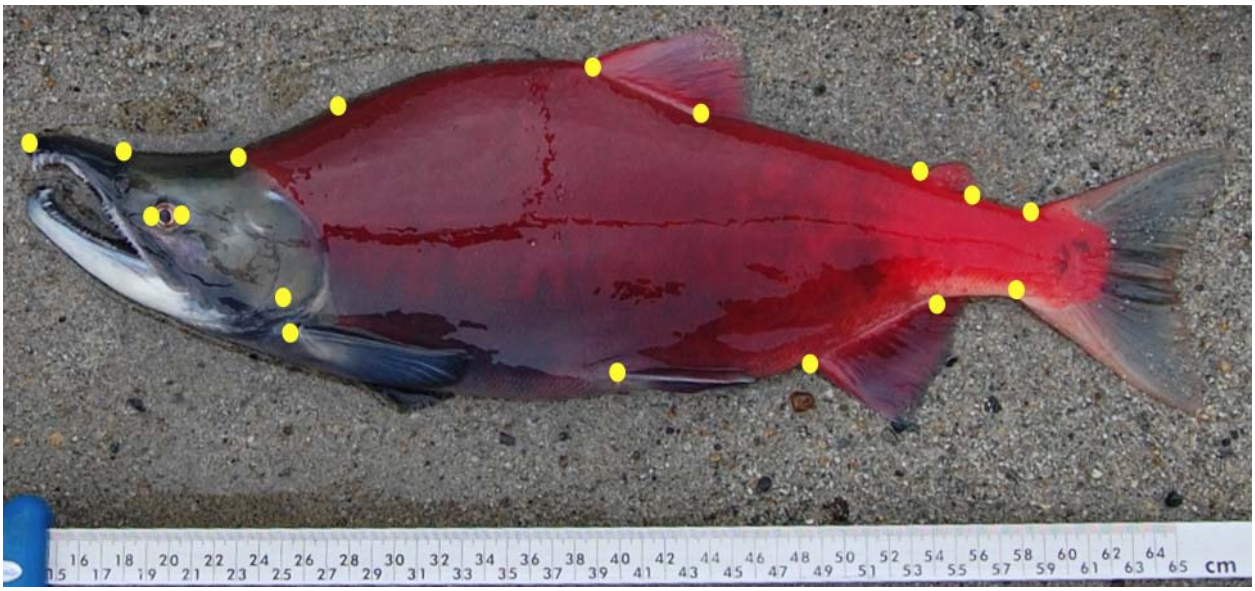

Figure 2. Landmarks used in geometric morphometric analysis.

We performed a generalized Procrustes superimposition to remove shape variation attributable to orientation and relative size of the image. The cumulative frequency distribution of individual deviations from average shape (measured as Mahalanobis distance) was compared to that of a cumulative multivariate normal distribution to identify gross outliers. To minimize the effects of allometry, we performed a pooled within-locality regression of Procrustes landmarks against body size (measured as centroid size of the 17 landmarks) and conducted subsequent analysis on residuals from the body-size regression. Principal components analysis (PCA) was performed on residuals; plots of the first and second principal components scores were inspected by each locality separately to identify potential outliers. Digitized images of individuals that fell outside of major clusters of PC scores were inspected visually; if digitization error was suspected, images were re-digitized, and if photo quality was suspected to be the source of deviation, these individuals were dropped from the analysis and the PCA was recalculated.

Canonical variate analysis (CVA) was performed on residuals of the body-size regression with individuals grouped by locality; this method finds axes of variation that maximize among-group variation while minimizing within-group variation (Albrecht 1980; Campbell and Atchley 1981). Implications of the CVA results for shape differences were visualized by comparing landmark coordinates of the average shape to those associated with a given CV score. Although we attempted to account for allometry analyzing body-size regression residuals, we further examined the effect of body size on shape by regressing CV scores against body length (MEHP).

As CVA purposefully maximizes the degree of variance among groups, we further analyzed the PCA on size-regression residuals as this method does not take into account prior information about group membership. We conducted an ANOVA on PC scores of the major principal component axes by drainage (Holitna vs. Telaquana) and spawning biotope (river, creek, beach) to determine the significance of morphological differences among groups.

Genetic diversity

DNA was extracted from ethanol-preserved fin clips as described in McPhee et al. (2007). We amplified genotypes at 14 microsatellite loci (Table 1), including loci used by Habicht et al. (2007) in Bristol Bay populations to enable direct comparison of results. Three multiplex groups of loci were amplified using PCR and amplification products were diluted, dried, and sent to the Murdock Sequencing Facility (The

University of Montana) for fragment analysis on a 3130xl Genetic Analyzer (Applied Biosystems). Genotypes were scored using GeneMapper v. 3.7 (Applied Biosystems). Deviations from Hardy-Weinberg expected proportions and gametic equilibrium were evaluated in GENEPOP (Raymond & Rousset 1995); P-values for multiple hypothesis tests were adjusted using the Benjamini and Yekutieli (2001) false discovery method.

Table 1. Allele size range, polymorphism, and source of microsatellite loci used in this study.

Locus	Size range (bp)	Total no. alleles	Mean alleles/ sample	Source
μSat60	117-133	5	4.1	Estoup et al. 1993
Ots100	147-201	16	8.8	Nelson and Beacham 1999
Ots107	106-130	7	4.9	Nelson and Beacham 1999
One102	203-255	14	10.5	Olsen et al. 2000
One105	122-152	9	3.5	Olsen et al. 2000
One108	181-245	17	13.1	Olsen et al. 2000
One109	123-183	13	10.5	Olsen et al. 2000
One111	192-328	31	16.8	Olsen et al. 2000
Oneμ8	193-209	8	4.8	Scribner et al. 1996
Oneμ14	131-183	14	6.3	Scribner et al. 1996
Oneμ18	169-209	8	4.3	Scribner et al. 1996
Oneμ21	246-250	2	1.8	Scribner et al. 1996
Oki1a	114-122	3	2.4	Smith et al. 1998
Oki1b	139–161	4	3.1	Smith et al. 1998

Genetic diversity was quantified using expected heterozygosity (probability that two alleles drawn at random from the sample will be non-identical) and allelic diversity (number of alleles per locus) adjusted for different sample sizes using rarefaction (HP-RARE, Kalinowski 2005). Multi-locus F_{ST} (Weir & Cockerham 1984) was calculated to quantify the degree of genetic differentiation between sample pairs; we also used a G-test (Goudet et al. 1996) to test for significant differentiation between sample pairs. Genetic distance and geographic distance (in river kilometers, or 'as the fish swims') were calculated between sample pairs to compare the degree of genetic differentiation by geographic distance in each drainage. We also compared pairwise morphometric distance (measured as Mahalanobis distance based on multivariate, size-corrected landmark data, see above in Morphometric diversity) to pairwise genetic distance to determine the degree to which morphological differences were correlated with genetic distances.

Overall ecotypic diversity: Holitna vs. Telaquana

For a number of ecotypic traits (body size, body depth, egg size) and habitat variables (vertical hydraulic gradient, habitat depth, velocity, temperature, conductivity, and sediment size), we compared diversity between the drainages by calculating coefficients of variability (which is the standard deviation divided by the absolute value of the mean, and represents a standardized unit of variability) and comparing them among sites and among drainages.

Comparison to Bristol Bay populations

Morphometric data from Holtina and Telaquana samples were compared to those in Bristol Bay (data originally reported in Quinn et al. 2001). We transformed body depth to a size-adjusted metric by scaling each individual male's body depth to a MEHP length of 450 mm, following the methods of Blair et al. (1993) and Quinn et al. (2001). We then compared mean size-adjusted body depth and coefficients of variability to determine how Kuskokwim sockeye populations compared to Bristol Bay populations, and

we determined the relationship between habitat depth and body depth, previously described for Bristol Bay populations by Quinn et al. (2001), for Kuskokwim samples. We compared genetic differentiation in the Kuskokwim to that of Bristol Bay by calculating locus-specific F_{ST} (a measure of genetic differentiation) and comparing those to locus-specific F_{ST}s for Bristol Bay presented in Habicht et al. (2007).

VI. RESULTS:

Habitat diversity

Mean (and standard deviation values) for physical habitat variables (vertical hydraulic gradient, depth, velocity, and sediment size) by locality are shown in Table 2 and Figure 3. Temperature and conductivity are presented in Table 2 and Figure 4. All habitat measures differed significantly by locality ($p<1.0x10^{-8}$ for all). All sites were dominated by upwelling (positive vertical hydraulic gradient values), although we did detect downwelling at a few points at the HOL and CHU sites in the Holitna drainage (Figure 3a). The inlet creek localities in Telaquana Lake were the most shallow. Velocities were low (<10 cm/s) except for KOG and OUT sites. Most sites were dominated by high percentage of fines covering the substrate prior to spawning activity, with the exception of OUT and SWB sites in Telaquana, which had negligible cover of fines. Underneath the fine sediments, sites were dominated by gravels (mean particle size < 64 mm), except for SWB which was dominated by cobbles. Temperature and conductivity varied greatly among sites, with the lowest temperature found at the BCR and the highest at PCR, and with CHU and BCR showing greater conductivity than other sites.

Table 2. Mean, standard deviation (std.), and sample size of physical habitat variables by drainage and locality.

Drain.	Locality	Vertical hydraulic gradient			Depth (cm)			Velocity (cm/s)		
		Mean	Std.	N	Mean	Std.	N	Mean	Std.	N
Holitna	KOG	0.16	0.18	16	51	13.1	4	36.3	16.2	4
	HOL	0.29	0.36	15	34	11.5	8	3.6	6.3	8
	CHU	0.06	0.23	16	31.4	6.4	8	5.4	4.4	8
Telaq.	OUT	0.33	0.32	15	27.9	6.6	8	36.2	16.8	8
	SWB[a]	0.34	0.2	16	>100	--	8	0	0	8
	UPB	0.69	0.29	16	49.9	6.5	8	0	0	8
	BCR	0.38	0.1	16	6.1	3.3	8	2.4	3.6	8
	PCR	0.39	0.16	16	9.3	2.7	8	4.7	5.2	8

		Temperature (°C)			Conductivity (µS)			Sediment size (mm)			
Holitna	KOG	Mean	Std.	N	Mean	Std.	N	Mean	Std.	N	% Fines
	HOL	10	0.17	4	54.3	1.4	4	46	42.1	100	75
	CHU	11.4	0.89	8	66.4	1.6	8	19.3	15.2	100	100
		10.3	0.89	8	83.6	4	8	28.7	21.1	100	100
Telaq.	OUT										
	SWB[a]	12	0.05	8	54.9	1.6	8	22.3	7.5	100	0
	UPB	11.1	0.21	8	51.6	0.3	8	109.3	46.4	100	0
	BCR	9.1	0.16	8	58.8	2	8	32.2	25.3	100	100
	PCR	5.9	0.45	8	82.4	1.1	8	29.6	10.3	100	80
		12.7	0.28	8	51.2	0.6	8	38.6	14.5	100	80

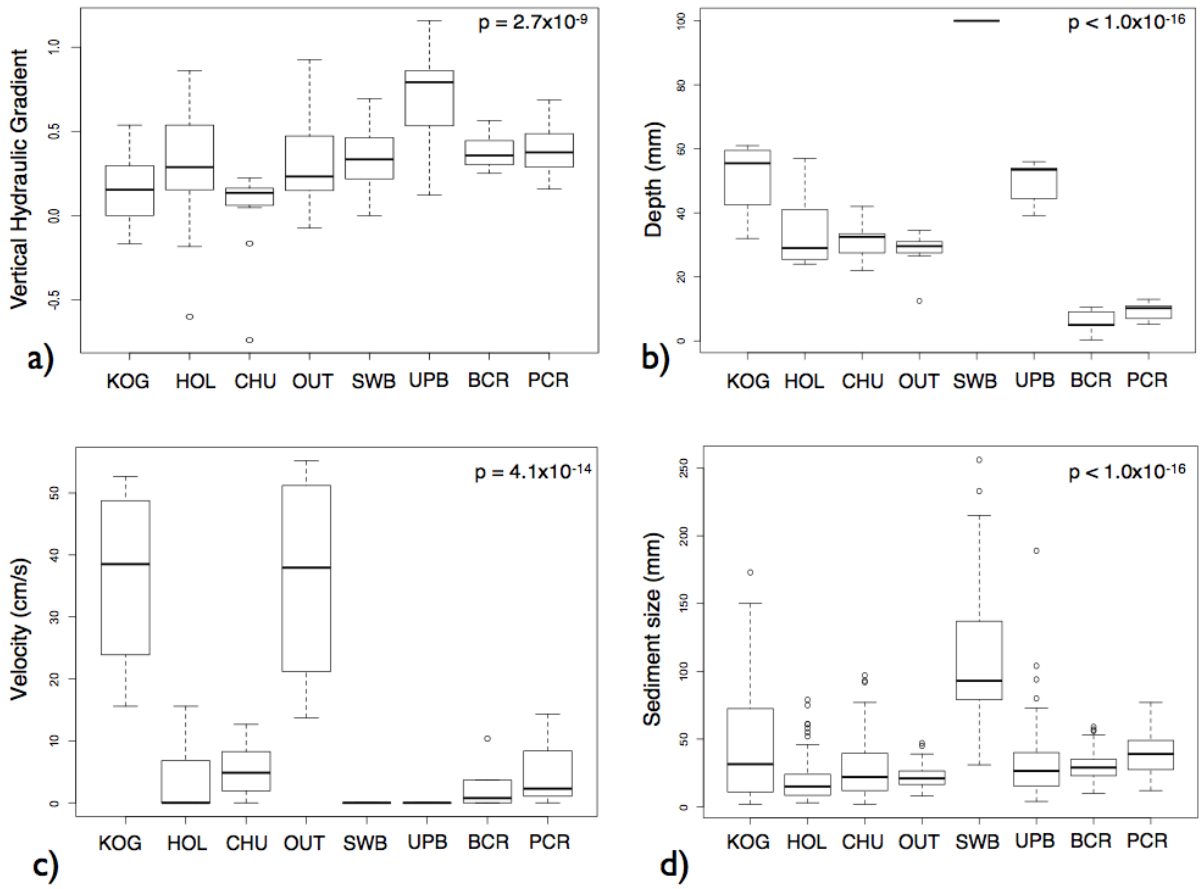

Figure 3. Boxplots of physical habitat variables, and p-values for ANOVA, by locality.

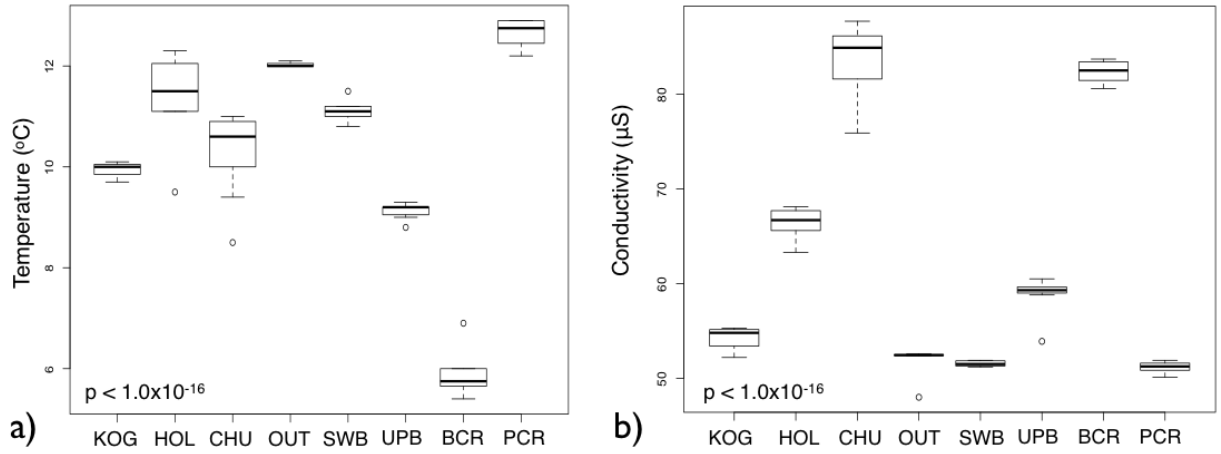

Figure 4. Boxplots of water quality variables, and p-values for ANOVA, by locality

Morphometric diversity

We obtained images suitable for digitization from 373 males (55 KOG; 32 HOL; 35 CHU; 52 OUT; 41 SWB; 58 UPB; 62 BCR; and 38 PCR). Following Procrustes fit, the cumulative frequency distribution of individual Mahalanobis distances from average shape approximated that of a cumulative multivariate normal distribution. Exclusion of the individual with the largest deviation from average shape did not substantially improve the fit of the curve, so all individuals were retained in the analysis at that point. Examination of digitized photographs of individuals that fell outside of the cluster of PC1 vs. PC2 plots for each locality (data not shown) resulted in six individuals being excluded from the analysis: one each from HOL, KOG, PCR, and UPB, and two from BCR, leaving a total sample size of 367 males.

Canonical variate analysis found clear morphological distinction among drainages and spawning biotopes. Canonical variate axes 1, 2 and 3 explained 53.8%, 21.4%, and 10.4% of overall variation in morphological variation, respectively (after accounting for body size). The first two axes, CV1 and CV2, separated three groups: Holitna River (HOL, KOG, CHU), Telaquana outlet (OUT), and Telaquana inlet and beach spawners (SWB, UPB, BCR, PCR) (Figure 5). Holitna males (positive CV1 scores) were distinguished from Telaquana males by a shorter, more upturned snout and a deeper body (Figure 6); Telaquana males spawning in the outlet (positive CV2 scores) were distinguished from other Telaquana males by their deeper bodies, larger humps, and more upturned snouts (Figure 5c). The third canonical variate (CV3) separated Telaquana inlet creek males (PCR and BCR) from Telaquana beach-spawning males (UPB and SWB); inlet creek males (positive CV3 scores) had narrower bodies than did beach-spawning males (negative CV3 scores) (Figure 6). Mean and standard deviation in scores for CV1-CV3 by locality are shown in Table 3; loadings (canonical coefficients) by landmark coordinate are given in Appendix A.

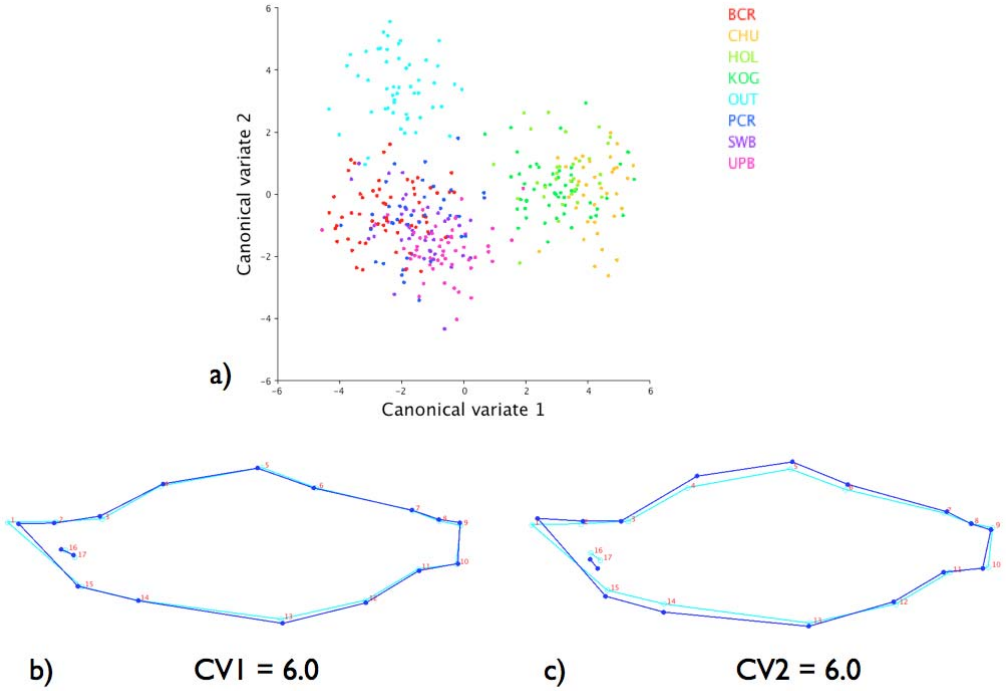

Figure 5. a) Scores for canonical variates 1 and 2, showing separation of Holitna males, Telaquana outlet males, and Telaquana inlet/beach-spawning males; b) shape associated with individuals with positive CV1 scores (Holitna males); c) shape associated with positive CV2 scores (Telaquana outlet males). For (a) and (b), light blue line is the consensus shape while the dark blue line is the shape associated with the respective canonical variate score.

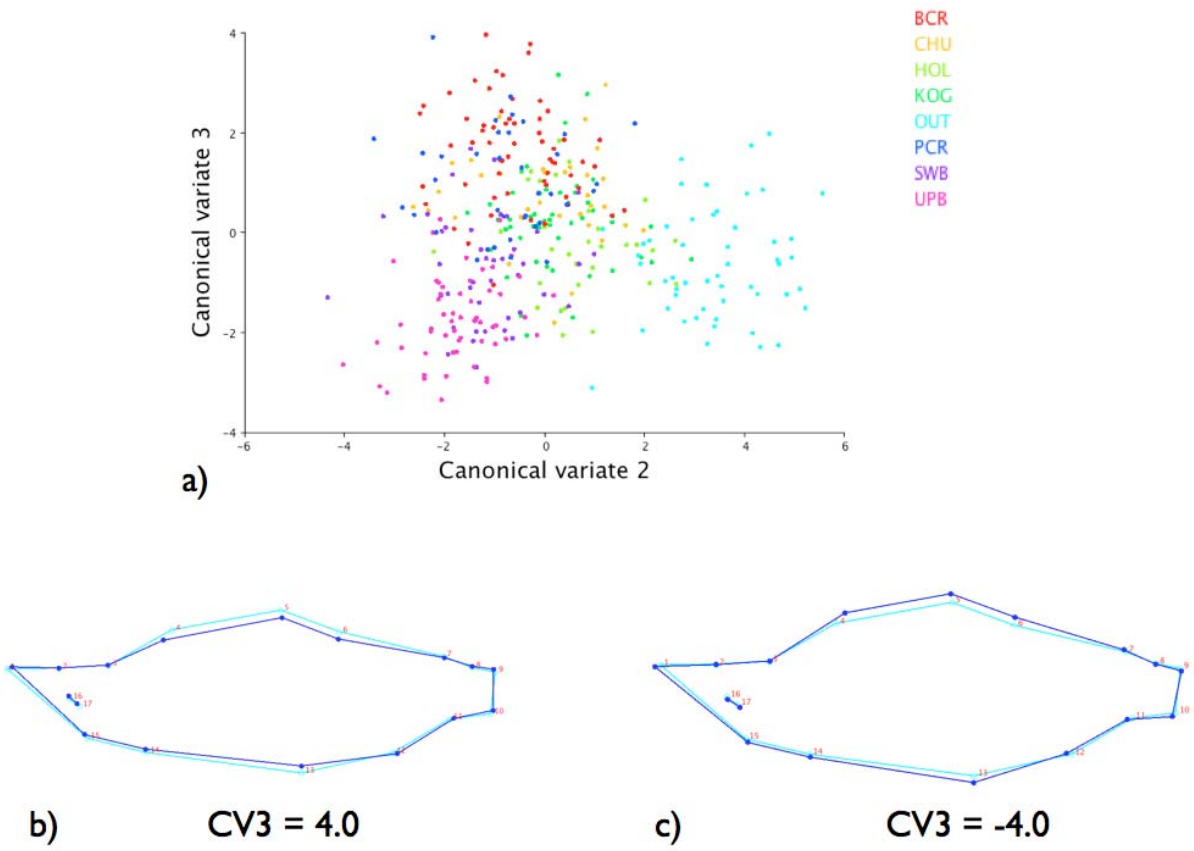

Figure 6. a) Scores for canonical variates 2 and 3, showing separation of Telaquana inlet creek males (BCR, PCR) from Telaquana beach-spawning males (UPB, SWB); b) shape associated with individuals with positive CV3 scores (Telaquana inlet creek males); c) shape associated with negative CV3 scores (Telaquana beach-spawning males). For (a) and (b), light blue line is the consensus shape while the dark blue line is the shape associated with the respective canonical variate score.

Table 3. Mean and standard deviation in scores for morphometric CV1-CV3 by locality.

Drainage	Locality	CV1		CV2		CV3	
		Mean	SD	Mean	SD	Mean	SD
Holitna	KOG	3.064	1.081	0.225	0.887	0.155	0.973
	HOL	3.237	0.924	0.678	1.042	-0.243	1.006
	CHU	4.272	0.671	-0.025	1.191	0.707	0.923
Telaquana	OUT	-2.112	0.927	3.435	1.072	-0.64	1.106
	SWB	-1.436	0.957	-1.164	1.011	-0.735	1.062

	UPB	-0.787	1.103	-1.728	0.817	-1.738	0.851
	BCR	-2.44	1.067	-0.582	0.949	1.651	1.019
	PCR	-1.497	1.059	-0.804	1.136	1.024	1.057

Principal components analysis on size-regression residual landmarks did not account *a priori* for drainage or spawning locality, but nonetheless supported results of the CVA. PC1 was associated with snout length/angle and body depth, with Telaquana outlet (OUT) males being distinguished from the other males by deeper bodies and longer and slightly more downturned snouts. Locality was significantly associated with PC1 score, but drainage was not (ANOVA, $p < 0.0001$ and $p = 0.60$, respectively, df = 366). Both drainage and locality were significantly associated with PC2 scores (ANOVA, $p < 0.0001$ for both, df = 366). Holitna males had more positive PC2 scores, also showing deeper bodies and more upturned snouts; however there was considerable variation among sites in PC2 scores. Variation in snout length was largely reflected in PC3, which was significantly associated with both locality and drainage (ANOVA, $p = 0.002$ and $p < 0.0001$, respectively, df = 366); Holitna males had shorter snouts (more negative PC3 scores). Mean and variance in scores for PC1-PC3 by locality are shown in Table 4; loadings by landmark coordinate for PC1-PC3 are given in Appendix B.

Drainage	Locality	PC1		PC2		PC3	
		Mean	SD	Mean	SD	Mean	SD

Table 4. Mean and standard deviation for morphometric PC1-PC3 scores by drainage and locality.

Holitna	KOG	-0.008	0.018	0.002	0.013	-0.011	0.009
	HOL	0.012	0.014	0.012	0.012	-0.011	0.010
	CHU	0.004	0.017	0.008	0.016	-0.012	0.010
Telaquana	OUT	-0.025	0.022	0.003	0.018	0.0003	0.009
	SWB	0.003	0.014	0.007	0.014	0.007	0.011
	UPB	-0.005	0.013	-0.010	0.014	0.008	0.008
	BCR	0.014	0.014	-0.011	0.012	0.006	0.007
	PCR	0.014	0.015	-0.001	0.013	0.007	0.010

Size and age diversity

Due to sampling constraints, we were unable to obtain sufficient otolith samples from each of our sampling sites. Instead, we were able to sample otoliths from the Holitna River at Ignatti weir (downstream of KOG but upstream of CHU and HOL). From Telaquana Lake, we obtained otoliths at the OUT and SWB sites as well as from the upper end of the lake. These upper Telaquana Lake collections included BCR, PCR, and UPB sites (and other, unsampled spawning localities); however individual carcasses could not be assigned to creek or beach spawning biotopes due to downstream drift and displacement by bears. Otoliths deemed by the reader to be of "questionable" quality were dropped from the analysis. This left a total of 492 otoliths (121 from Holitna, 77 from OUT, 20 from SWB, and 274 from upper Telaquana Lake).

Ages ranged from 1.1 to 1.4 and 2.2 to 2.3, with greater age variability in males than in females (Figure 7). Individuals with two freshwater increments were only found within Telaquana Lake (upper Telaquana Lake and SWB); otoliths from Telaquana OUT and from the Holitna drainage all had a single freshwater increment. Otoliths from SWB were not included in statistical analysis due to small sample size. However, the distribution of ages differed significantly among the other localities (Holitna River, upper Telaquana Lake, and Telaquana OUT) for both sexes (Fisher's exact test; $p < 0.001$, df =10 for both males and females).

Due to the low numbers of 2.x individuals and the inability to distinguish adult body length (MEHP) by freshwater increment (data not shown), we analyzed body length by number of saltwater increments (Figure 8). Three- and four-salt individuals of either sex were not readily distinguished by body length at any locality. Two-salt males were clearly distinguished from older males in the Holitna (<400 mm MEHP). One-salt males were clearly distinguished from older males in Telaquana (OUT and upper samples; < 350 mm MEHP), but the distinction between two- and three-salt males was not as clear. Interestingly, two-salt males from upper Telaquana Lake had a higher mean and variance in body size than did males from Telaquana OUT, and both had a higher mean size than did Holitna two-salt males (Figure 7). However, comparisons between drainages were complicated by differences in return year (2008 in the Holitna, and 2009 in Telaquana).

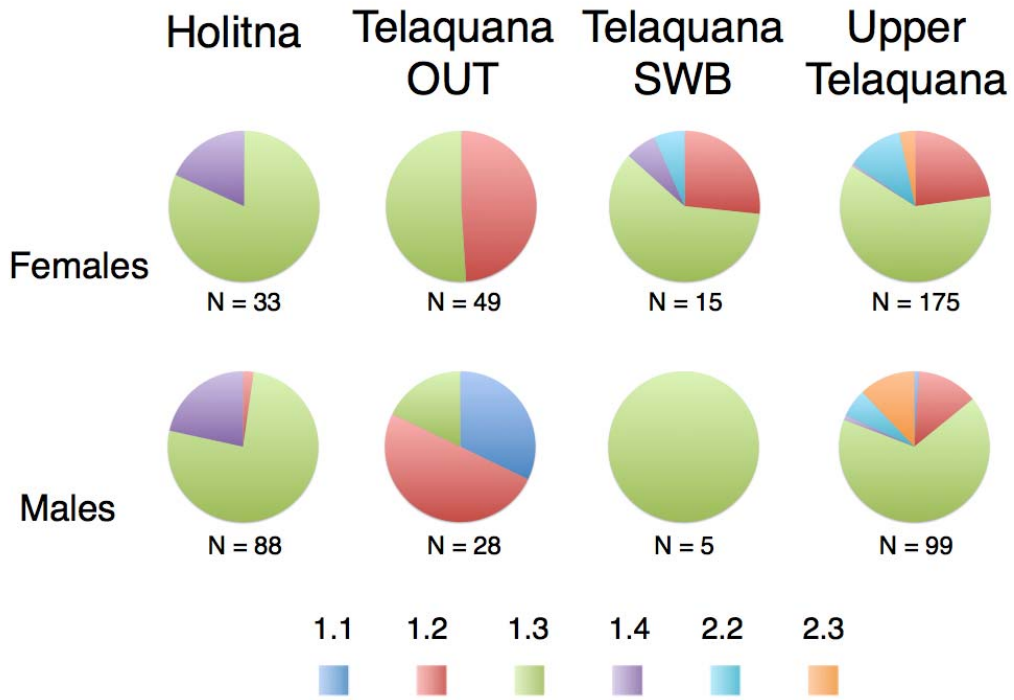

Figure 7. Distribution of age classes determined from otolith samples, by locality and sex.

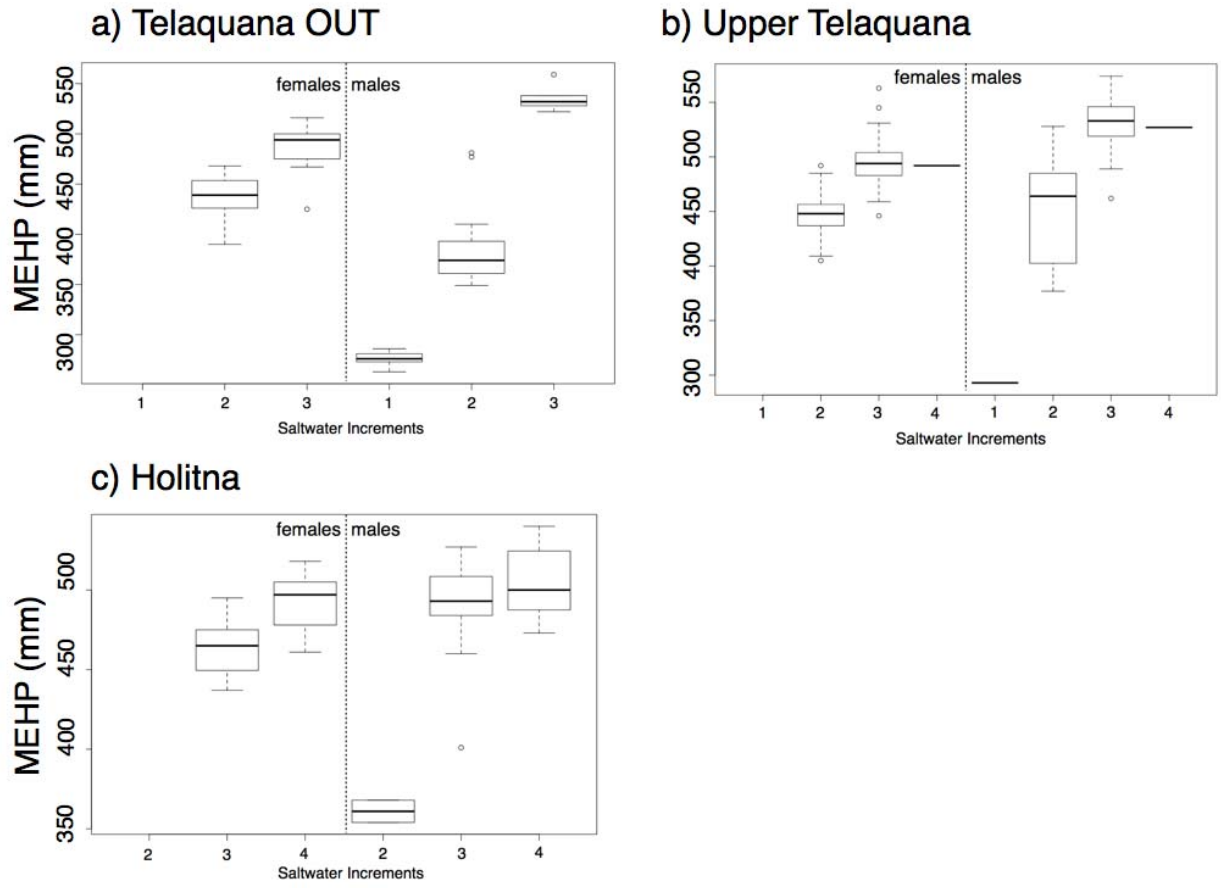

Figure 8. Body length (MEHP, mm) by sex and saltwater age.

Because of the lack of clear body-size differences among older age classes, we limited our analysis of spawning adult samples to size diversity as opposed to age-class diversity. The distributions of body length (MEHP) by locality and sex are shown in Figure 9. Drainage and locality had highly significant effects on size, both for males and females (Table 5). Telaquana females were generally larger than Holitna females, with beach-spawning (SWB and UPB) being the largest, followed by inlet-creek spawning females (PCR and BCR), and outlet spawners (OUT) being the smallest and similar in size to Holitna females (Figure 9a). Male size was much more variable, with the greatest amount of variation in Telaquana. Within Telaquana, beach spawners (SWB and UPB) were the largest and inlet creek spawners (PCR and BCR) were smallest. Holitna males were large, with less variance around the mean (Figure 9b).

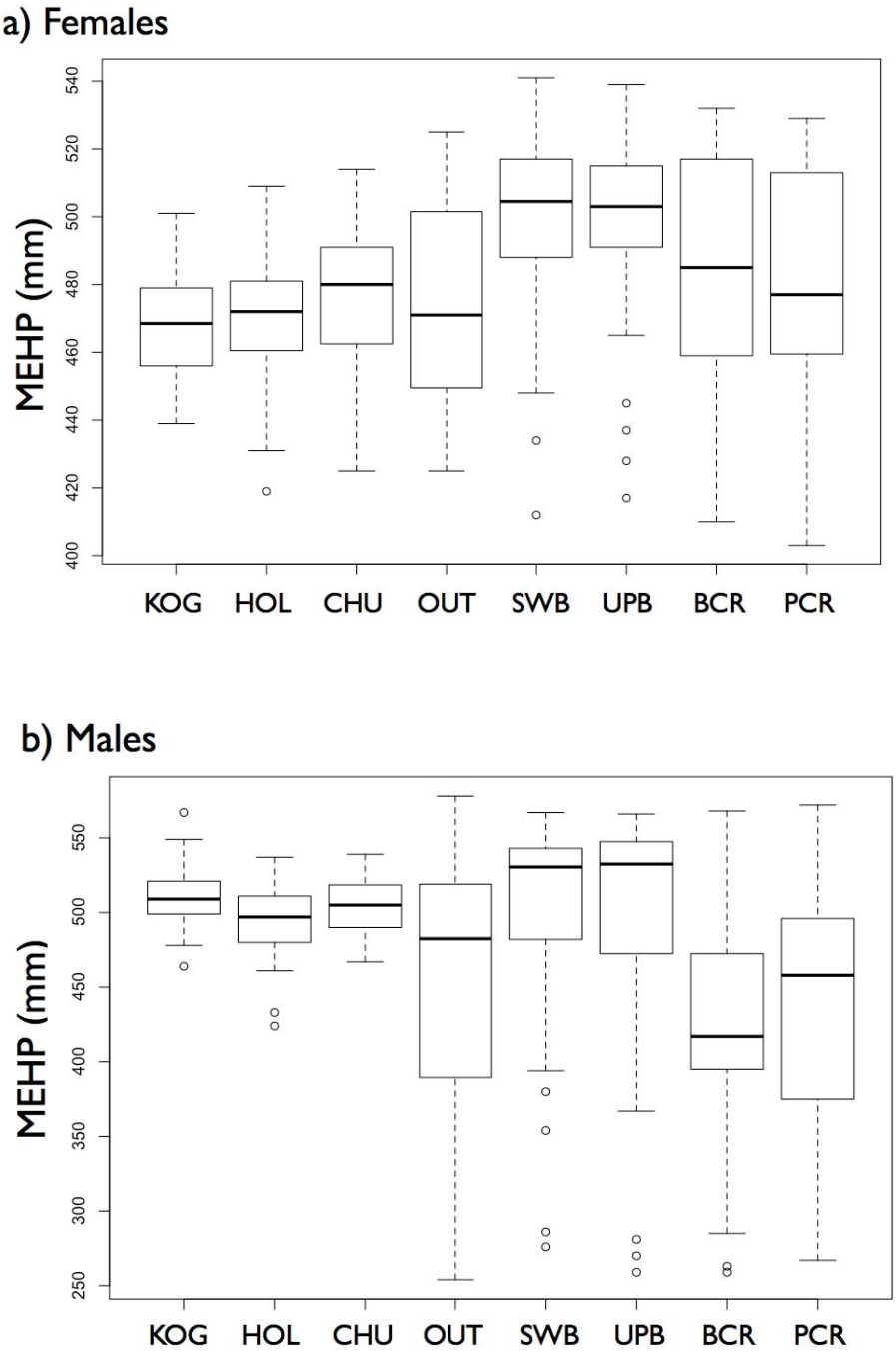

Figure 9. Lenth (MEHP) b y locality. a) females; b) males.

Table 5. Results of ANOVA of drainage and locality on body length (MEHP) by sex.

Factor	Sum of Squares	Mean Squares	F	P	Df
Females					
Drainage	24034	24034.0	34.1526	1.183e-08	1
Locality	21889	3648.2	5.1842	4.018e-05	6
Residuals	242080	703.7			344
Males					
Drainage	150563	150563	36.889	3.056e-09	1
Locality	292417	48736	11.941	2.779e-12	6
Residuals	1538732	4082			377

Egg size diversity

Egg diameter increased significantly with body length ($p = 1.5 \times 10^{-8}$, df = 248). Analysis of covariance indicated that the relationship between mean egg diameter and body length differed significantly among localities in intercept ($p = 3.0 \times 10^{-14}$, df = 7) but not in slope (p = 0.40, df = 7; Figure 10). Although variation in mean egg diameter was modest (Table 6), significant differences among localities persisted after accounting for variation in body length (ANOVA, $p = 2.7 \times 10^{-14}$, df = 7). Mean egg size was not significantly related to mean sediment size (p = 0.35).

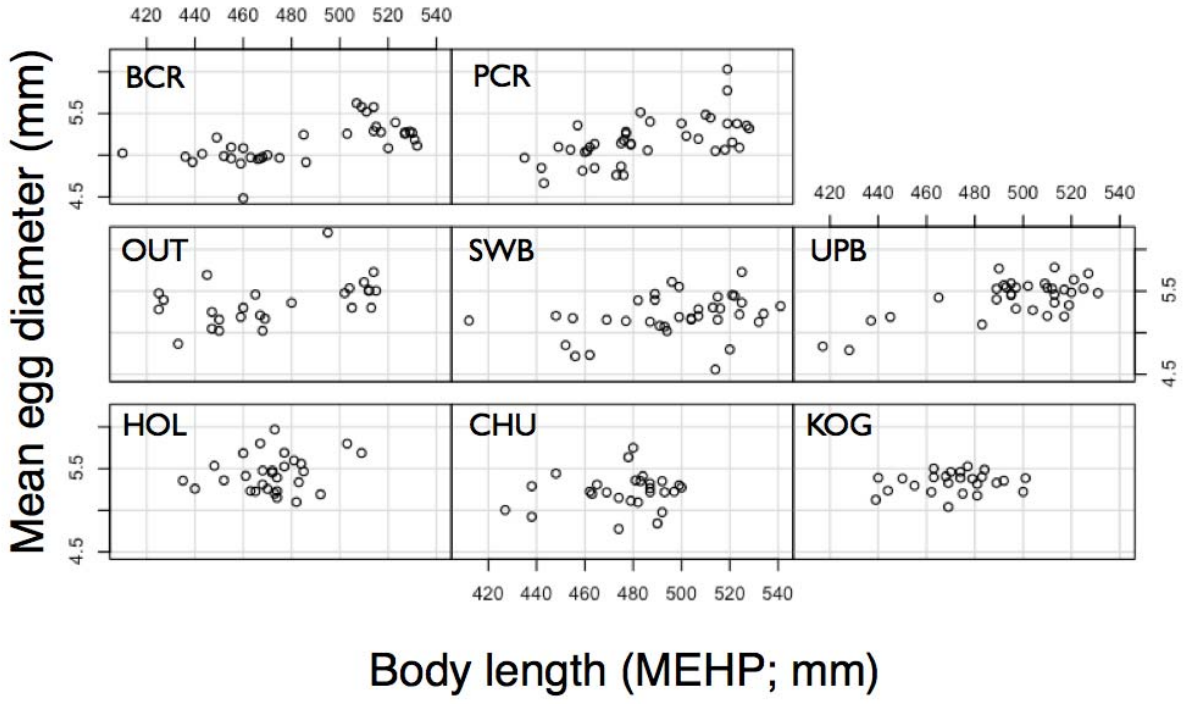

Figure 10. Mean egg diameter versus female body length (MEHP) by locality.

Table 6. Mean and standard deviation in egg size by drainage and locality.

Drainage	Locality	Mean egg diameter (mm)	Standard deviation	N
Holitna	KOG	5.34	0.12	25
	HOL	5.44	0.22	29
	CHU	5.23	0.21	27
Telaquana	OUT	5.37	0.27	26
	SWB	5.20	0.25	36
	UPB	5.42	0.23	33
	BCR	5.14	0.24	35
	PCR	5.17	0.27	39

Genetic diversity

Allele frequencies, sample sizes, and results of tests for deviation from Hardy-Weinberg expected proportions by locus and locality are given in Appendix C. We detected 11 instances of significant departures from Hardy-Weinberg expected proportions. All departures were positive F_{IS} values, seen in UPB (*Oki1a, One14*), SWB (*Oneμ14*), PCR (*One102*), CHU (*Oneμ8*), KOG (*Ots100*), and HOL (*One102, One108, Ots100, One111, Oneμ8*). As significant departures were not consistent across loci, we had no cause to suspect null alleles. Potential causes of the large number of positive F_{IS} values in the HOL sample are discussed in McPhee et al. (2009b). Over all samples combined, *One109* was in significant gametic disequilibrium with both *Ots100* ($p < 0.0001$) and *One111* ($p = 0.005$); therefore *One109* was dropped from further analyses, with the exception that we calculated overall F_{ST} for *One109* to allow comparison to Bristol Bay results (Habicht et al. 2007).

Holitna River samples had higher genetic diversity (measured as expected heterozygosity and average allelic diversity) than did Telaquana samples (with OUT having the lowest genetic diversity); however differences in diversity were not large (Figure 11). Within the Holitna River, samples CHU, HOL, and KOG did not differ statistically in allele frequencies. Within Telaquana Lake, all sample pairs were statistically different from each other in allele frequencies except for the two inlet creek-spawning samples PCR and BCR. Pair-wise F_{ST} values ranged from 0.0007 (BCR-PCR) to 0.169 (CHU-OUT). Results of G-tests for pair-wise differentiation in allele frequencies and pair-wise F_{ST} values are shown in Table 7. Genetic distance between samples was greater over shorter distances in Telaquana Lake when compared to Holitna River samples (Figure 10). Pair-wise morphological distance between samples, measured as Mahalanobis distance, increased with genetic distance between sample pairs (Mantel test, $p = 0.001$; Figure 11).

Table 7. P-values for G-tests for pair-wise genetic differentiation (above diagonal) and pair-wise F_{ST} values (below diagonal).

	KOG	HOL	CHU	OUT	SWB	UPB	BCR	PCR
KOG	--	0.018	0.019	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
HOL	0.006	--	0.137	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
CHU	0.010	0.005	--	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
OUT	0.161	0.150	0.169	--	<0.0001*	<0.0001*	<0.0001*	<0.0001*
SWB	0.129	0.129	0.151	0.037	--	0.003*	<0.0001*	0.0002*
UPB	0.117	0.110	0.132	0.041	0.006	--	<0.0001*	<0.0001
BCR	0.115	0.114	0.132	0.052	0.010	0.008	--	0.035
PCR	0.120	0.118	0.136	0.035	0.003	0.008	0.0007	--

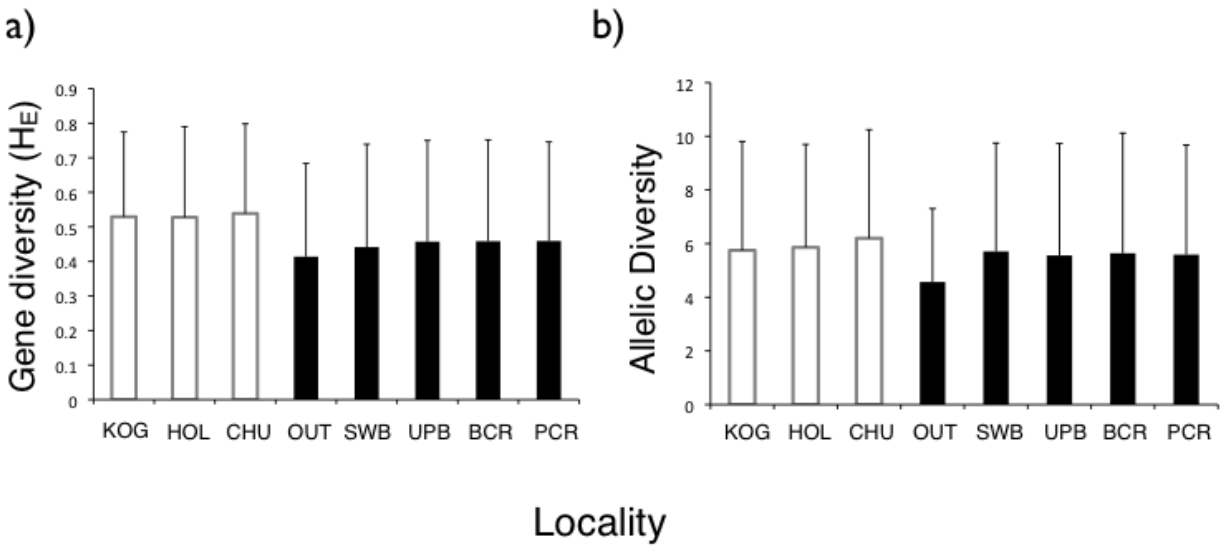

Figure 11. Genetic diversity by drainage (open bars, Holitna; solid bars, Telaquana). a) gene diversity (expected heterozygosity); b) allelic diversity, averaged over loci.

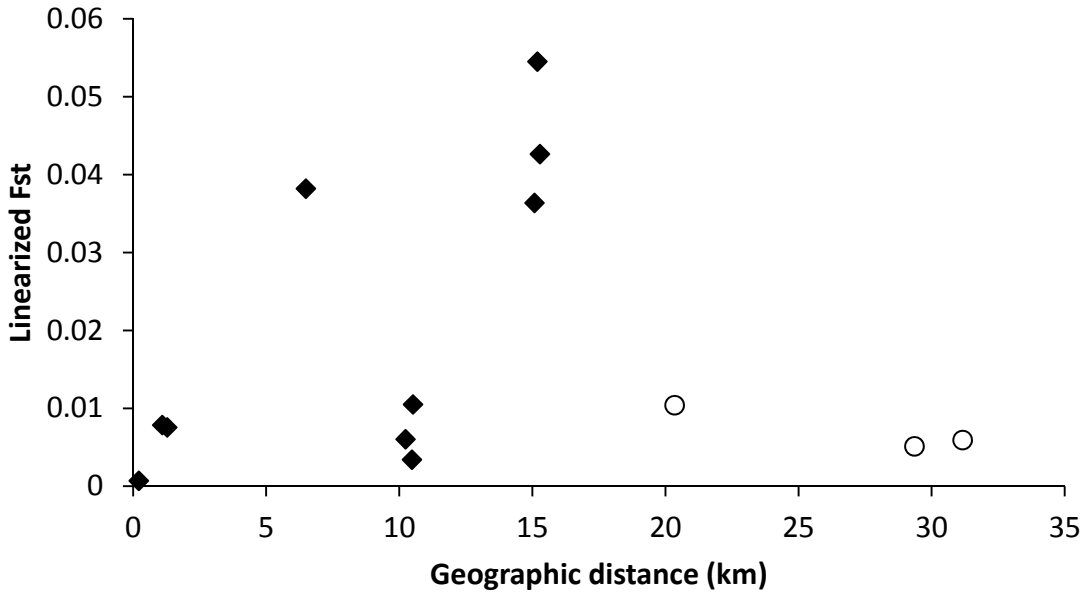

Figure 12. Pair-wise genetic (linearized Fst) versus geographic distance. Black diamonds, Telaquana samples; open circles, Holitna samples.

Overall ecotypic variation: Holitna vs. Telaquana

Coefficients of variability for ecotypic variables (female and male length, male size-adjusted body depth, and egg diameter) and habitat variables (vertical hydraulic gradient, habitat depth, velocity, temperature, conductivity, and sediment size) by locality within the Kuskokwim samples are show in Figure 13. In general, ecotypic variability was greater in Telaquana spawning sites, which supported greater female size diversity, substantially greater male size diversity, and greater egg size diversity within sites. Conversely, Holitna supported greater diversity in habitat variables within sites, in particular vertical hydraulic gradient and temperature. However, Telaquana supported greater spawning biotope complexity, with spawners found in river, creek and beach biotopes, whereas in the Holitna we only found spawning in river biotopes.

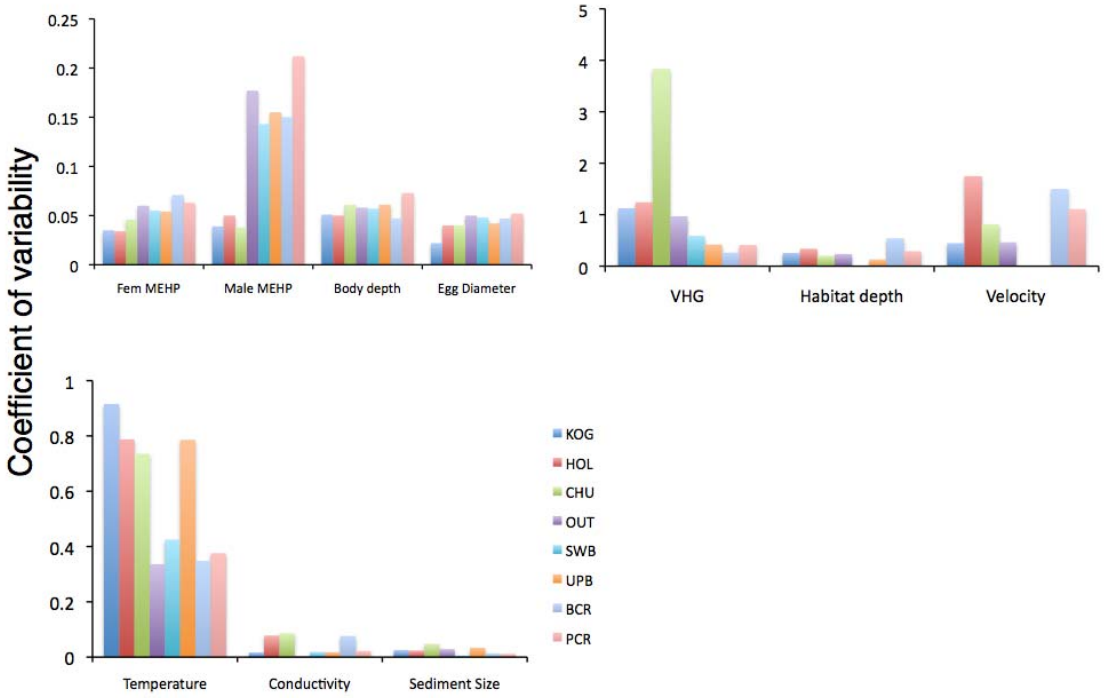

Figure 13. Diversity (coefficient of variability) within and among localities for ecotypic and habitat variables.

Comparisons to Bristol Bay

Size-adjusted body depth by spawning biotope (river, beach, and creek) and drainage (Kuskowkim, Iliamna, and Wood River) are shown in Figure 14. Body depths were similar across drainages with the exception that sockeye spawning in river habitats in the Kuskokwim had greater size-adjusted body depths when compared to Bristol Bay samples. Kuskokwim (Holitna + Telaquana) samples showed less variability in mean body depth than did Bristol Bay (Iliamna + Wood River) samples (CV = 0.06 for Kuskokwim and 0.08 for both Iliamna and Wood River).

Habitat depth was highly correlated with size-adjusted body depth across all samples ($p < 0.0001$; Figure 15). ANCOVA indicated that the intercept of the relationship between habitat depth and size-adjusted body depth differed between Kuskokwim and Bristol Bay samples ($p = 1.4 \times 10^{-9}$), and there was marginal evidence for an interaction between drainage and habitat depth ($p = 0.04$).

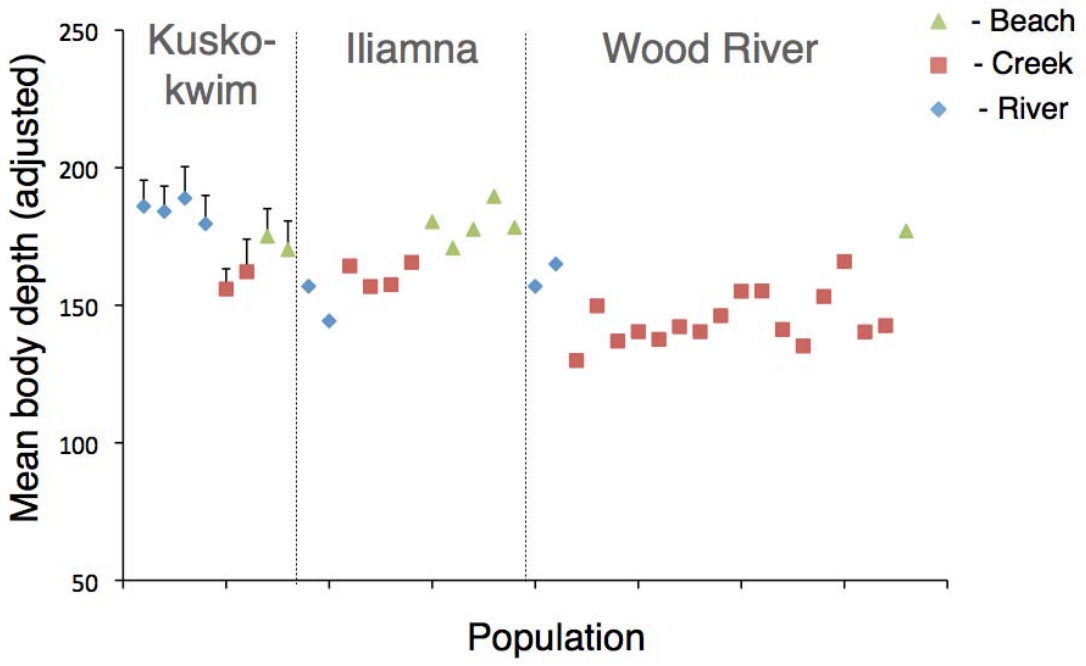

Figure 14. Mean body depth (adjusted to a common size of 450 mm MEHP) by drainage and spawning biotope.

Locus-by-locus F_{ST} allowed comparisons between our Kuskokwim samples (Holitna + Telaquana) to Bristol Bay samples (encompassing the Wood River, Nushagak, Iliamna, Naknek, and Egegik drainages). This analysis indicated that genetic differentiation among populations in the Kuskokwim was approximately twice that of differentiation observed among Bristol Bay populations (Table 8).

Table 8. Comparison of study-wide F_{ST} by locus between Kuskokwim (this study) and Bristol Bay (Habicht et al. 2007).

Locus	F_{ST} - Kuskokwim	F_{ST}– Bristol Bay
One102	0.023	0.017
One108	0.031	0.016
One109	0.085	0.021
One111	0.053	0.025
Ots107	0.058	0.023
Usat 60	0.128	0.028

VII. DISCUSSION:

By comparing the morphological, life history, and genetic diversity and structure of spawning sockeye salmon, as well as characteristics of spawning habitat, within and between two drainages in the Kuskokwim River, we were able to document considerable ecotypic and genetic variation within the basin.

First, there were clear-cut differences in adult sockeye salmon characteristics between the two drainages that we sampled. Holitna sockeye salmon were distinguished from Telaquana sockeye salmon morphologically, having shorter snouts and bodies not as deep as Telaquana sockeye (on average). They also showed slightly less age-class diversity (2-4 saltwater increments, as opposed to 1-4 saltwater increments in Telaquana). Holitna males were generally larger (dominated by saltwater age-3 and -4) than those in Telaquana (primarily saltwater age-2 and -3). Concurrent with less age-class diversity, Holitna males showed considerably less size variation when compared to Telaquana males; we observed no 'jacks' (<300 mm MEHP) employing a sneaking mating tactic in the Holitna, and in our live adult sampling, we did not capture any males < 400 mm MEHP. Selection for large body size in the river spawning biotopes of the Holitna might select against saltwater age-1 males; however the river biotope in Telaquana (OUT) supported jacks, so it is not clear why we saw the lack of saltwater age-1 fishes in Holitna. We also observed a lack of freshwater age-2 fishes in the Holitna; all were freshwater age-1. This is probably a result of their river-type juvenile life history (McPhee et al. 2009b); spending a second year rearing in the river is likely less energetically profitable than spending a second year rearing in a lake. Interestingly, we only observed freshwater age-2 individuals spawning within Telaquana Lake (beach and inlet creek habitats); all of the individuals we sampled in the outlet (OUT) were freshwater age-1.

The variation in size-corrected male body depth we observed in our study was on par with that observed in Bristol Bay (Quinn et al. 2001). However, most of the variation within the Kuskowkim was found in Telaquana. Since body depth correlates with spawning biotope (deeper in beach spawners, shallower in creek spawners; Quinn et al. 2001), the lack of variation in the Holitna is consistent with the lack of both beach and creek spawning biotopes in that system. Interestingly, the relationship between spawning biotope and body depth in the Kuskokwim differed from that observed in Bristol Bay: males spawning in river biotopes were actually deeper-bodied than beach spawners in the Kuskwim (Figure 14), on par with the deepest-bodies males from beach spawning sites in Lake Iliamna. Male body depth (after correcting for body length) was correlated with habitat depth, as has been observed for Bristol Bay populations (Quinn et al. 2001), but again, the relationship was different (statistically different intercept) in the Kuskokwim, with male body depth being greater for a given habitat depth when compared to samples from Bristol Bay. However, we did not measure habitat depth in exactly the same way as did Quinn et al. (2001), which might have contributed to the difference.

Unlike Bristol Bay, we found very little variation in egg size between localities within drainages and between the two drainages, although variation within localities was slightly higher in Telaquana compared to Holitna. The lack of variation in both egg size and sediment size probably explains why we failed to detect a relationship between sediment size and egg size, as has been documented for Bristol Bay populations (Quinn et al. 1995). In general, we did not see a lot of variation in female size, which as a tight correlate of egg size (Quinn et al. 1995) probably explains the lack of variation in egg size in our Kuskowkim samples.

The distribution of genetic diversity differed considerably between the two drainages. Both had similar levels of allelic diversity (number of alleles per locus, corrected for sample size), but Telaquana samples had lower heterozygosity. Genetic differentiation among sites within Telaquana was greater over smaller spatial scales than differentiation within Holitna. This pattern of lower heterozygosity and greater genetic

differentiation is typical of lake-type populations such as Telaquana, when compared to river-type populations such as Holitna (Wood et al. 2008, McPhee et al. 2009b), so this result is not surprising. We also detected considerable differentiation between sockeye spawning in the outlet of Telaquana (OUT) and spawning populations within the lake, including inlet tributaries. This level of genetic differentiation suggests that there is little gene flow between outlet spawners and those spawning within the lake. Such differences between outlet and inlet/within-lake spawners is expected, given their offspring must show diametrically opposed rheotactic responses to arrive at their rearing lake (sensu Brannon 1972). Note that this explanation relies on the assumption that offspring of outlet spawners do indeed rear in the lake; we did not explicitly address this assumption.

Genetic differentiation, based on loci shared with those reported in Habicht et al. (2007), was greater (roughly twice as large) among our Kuskokwim samples than among Bristol Bay samples, even though the Bristol Bay study spanned an area larger than our study area. This could be explained in several ways. First, gene flow among drainages could be greater in Bristol Bay than in the Kuskokwim. This seems a plausible explanation, given that the geography of drainages differs substantially between the two regions; Bristol Bay drainages are arrayed around the bay, whereas drainages within the Kuskokwim are arrayed linearly along the Kuskokwim River. A second explanation involves historical effects. Varnavskaya et al. (1994) found evidence that Telaquana Lake sockeye were closely related to Bristol Bay sockeye. Given the low topography separating Telaquana Lake from the headwaters of the Mulchatna River (McPhee, pers. obs.), it is not unlikely that Telaquana Lake was actually colonized from Bristol Bay sources, and other sockeye salmon rivers within the Kuskokwim (such as the Holitna and Kwethluk rivers) were colonized separately. Such differences in colonizing lineages could still be detected as high genetic variation among sites within the Kuskokwim.

To our surprise, morphological differences were correlated with neutral genetic divergence, both among sites within drainages and between sites from Holitna versus Telaquana. Although we had strong a priori reasons to suspect natural and sexual selection acting in shaping some morphological traits (e.g., male body depth), the major axis of variation between drainages was related strongly to snout length. It has been hypothesized that snout length should be under sexual selection (Quinn et al. 1995); yet it is also possible that snout length differences between Telaquana and Holitna fishes reflects neutral divergence between them. Snout length has been found to decrease with migration distance in salmon (Kinnison et al. 2003), the idea being that sexual selection drives an increase in snout length while increased migration distance decreases the amount of energy available to allocate to snout elongation. In the Kuskowkim we observed the opposite pattern; Holitna fishes, which are lower in the Kuskokwim and have a shorter migration distance, had the smaller snouts. This disparity could be related to historical factors: if Telaquana fish did come from a Bristol Bay source population, their ancestors would have had a much shorter migration distance than do contemporary Telaquana fishes and thus might have evolved larger snouts prior to colonization of Telaquana Lake.

Habitat diversity was expressed at two different scales. At the drainage scale, Telaquana exhibited much greater complexity in available spawning biotopes. Sockeye spawned in the outlet river, on beaches within the lake, and in inlet creeks, similar to what is found in Bristol Bay. Conversely, spawning in the Holitna River was essentially limited riverine biotopes, mainly in the form of side channels fed by erupting hyporheic water. Variation in smaller scale habitat measures *within* localities was greater in the Holitna, however. For example, point-to-point variation in vertical hydraulic gradient, velocity, temperature, and conductivity was greater in localities from the Holitna River. This complexity probably reflects the large influence of upwelling hyporheic water, which is a hallmark of active river floodplains (e.g., Stanford et al. 2005). All spawning localities we sampled, including beach spawning sites in Telaquana, were dominated by upwelling. We observed substantial cover of fine sediments at many of our sites; this observation highlights the importance of connectivity to hyporheic water for sockeye salmon incubation, regardless of spawning biotope.

Implications for Management

Male body depth and age-class variation are established indicators of biocomplexity in sockeye salmon, and diversity in these indicators is correlated with regional run stability via the portfolio effect (Hilborn et al. 2003, Schindler et al. 2010). Our study documented differences in diversity at these indicators between the Telaquana and Holitna drainages: greater diversity was found in Telaquana, likely due to the greater complexity in spawning biotopes present in this lake environment. Conversely, the Holitna, a riverine system, had limited spawning biotope, age-class, and morphological diversity. This suggests that over fishery time scales (e.g., 50-100 years), Telaquana runs might be more reliable (less variable) from year to year, while large fluctuations in returns to the Holitna might be expected. Unfortunately, we cannot yet test this prediction as Telaquana has only had an escapement project in place since 2010 (D. Molyneaux, ADF&G, pers. comm.). However, on longer time scales, the river-type form of sockeye salmon found in the Holitna has an important role to play in the long-term persistence of sockeye salmon within the Kuskokwim system. Wood et al. (2008) have hypothesized, based on patterns in genetic diversity and structure, that the lake-type sockeye salmon is more prone to local extinction and that the river-type sockeye salmon is more important for recolonization (discussed in the context of the Kuskokwim River in McPhee et al. 2009b). Taking a long view (10,000 year time scale), this suggests that despite limited ecotypic diversity, river-type sockeye salmon populations such as the Holitna and the Kwethluk rivers might eventually be important reservoirs of genetic diversity for future colonization and recolonization in the system. Thus both life history types need to be properly managed to ensure the long-term persistence of sockeye salmon in the Kuskokwim drainage. Continued support of escapement projects on both the Holitna and Telaquana Lake is necessary for such management.

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IX. DELIVERABLES:

Grant Reporting

McPhee, M. V. AYK: Ecotypic variation in AYK sockeye – Phase 1. Semiannual Report. November 2008.

McPhee, M. V. AYK: Ecotypic variation in AYK sockeye – Phase 1. Semiannual Report. May 2009.

McPhee, M. V. AYK: Ecotypic variation in AYK sockeye – Phase 1. Semiannual Report. November 2009.

McPhee, M. V. AYK: Ecotypic variation in AYK sockeye – Phase 1. Final Report. May 2010.

McPhee, M. V. AYK: Ecotypic variation in AYK sockeye – Phase 2. Semiannual Report. November 2010.

McPhee, M. V., T. P. Quinn, and J. A. Stanford. Ecotypic variation in AYK sockeye. 2011 Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative Project Final Product. June 2011. [this report]

Other Publications

McPhee, M. V., T. H. Tappenbeck, D. C. Whited, and J. A. Stanford. 2009. Genetic diversity and population structure in the Kuskokwim River drainage support the 'recurrent evolution' hypothesis for sockeye salmon life histories. Transactions of the American Fisheries Society 138:1481-1489.

Presentations/Outreach

McPhee, M. V. 2009. Ecotypic variation in Kuskokwim sockeye salmon stocks. Kuskokwim Interagency Meeting, Anchorage, AK.

McPhee, M. V. 2009. Origins and effects of ecotypic diversity in salmonids. Presented to the School of Fisheries and Ocean Sciences, University of Alaska Fairbanks. Juneau AK, 6 Apr, and Fairbanks AK, 8 Apr. (Invited talk; hosts Dr. Franz Mueter and Dr. Andrés Lopez.)

McPhee, M. V. 2009. Ecotypic variation in Kuskokwim sockeye salmon: AYK SSI project update. Alaska Chapter, American Fisheries Society meeting, Fairbanks, AK, 4 Nov.

McPhee, M. V. 2010. What underlies morphological diversity in salmonids, and why should we care? Presented to the School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau AK, 26 Feb. (Invited talk; host Dr. Keith Criddle.)

McPhee, M. V. 2010. Ecotypic variation in Kuskokwim sockeye salmon stocks: AYK SSI project update. Kuskokwim Interagency Meeting, Anchorage, AK, 30 Mar.

McPhee, M. V., T. P. Quinn, and J. A. Stanford. 2010. Ecotypic and genetic diversity within and among sockeye salmon populations from the Kuskokwim drainage of southwestern Alaska. Coastwide Salmonid Genetics, Boise, ID, 3 Jun [poster presentation].

McPhee, M. V. 2010. Ecotypic diversity in salmonids over disparate timescales. Presented to the School of Aquatic and Fisheries Sciences, University of Washington, Seattle, 14 October. (Invited talk; hosts Drs. Thomas Quinn and Nathan Mantua.)

Future deliverables
The final product of this study will be prepared as a manuscript for submission to a peer-reviewed journal such as *Canadian Journal of Fisheries and Aquatic Sciences* or *Transactions of the American Fisheries Society*.

X. PROJECT DATA:

Forthcoming.

A summary of the data collected during the project shall be included as a part of the project's Final Product in order to preserve the opportunity for other researchers and the public to access these data in the future. The summary shall: (1) provide a complete metadata description ("data about data") in a format compliant with the Federal Geographic Data Committee (FGDC) standards (see FGDC standards link) and/or the AYK SSI Research Coordinator will provide data information sheets to help the PI to encapsulate this information; (2) indicate the format of the available data collections; (3) identify the archive in which the data will be stored, or the custodian of the data (including contact name, organization, address, phone/fax, email, and web address (if applicable) where data may be acquired.) If the PI does not have access to an established appropriate data archive in which to store data, the AYK SSI Research Coordinator will work with PI to access and archive or store data with the AYK SSI.

Full Project Data: *We encourage data from routine research activities (data which do not require processing or manipulation) to be available regularly and in real or near-real time. The PI retains exclusive publication use of the data and developed models during the first year after the project's Final Product has been accepted. Full project data, including a data summary and full metadata in the format described above, will be available to other users after that period.* ***An electronic copy and two paper copies of complete project data will be submitted to the AYK SSI along with the Final Product.*** *As a condition of the project contract, it is required that all data requests by other researchers and the public be fulfilled in a timely manner.*

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XII. PRESS RELEASE:

"Biocomplexity" has been recognized as a hallmark of Bristol Bay sockeye salmon populations and a key to the long-term stability and success of this commercial fishery. Sockeye salmon in Bristol Bay consist of a complex of locally specialized populations that respond to environmental variation in unique ways. When viewed at the regional (fishery) scale, this diversity leads to enhanced stability, much as a diverse portfolio of stocks yields more stable economic returns than would an individual fund. However, Alaskans want to know if biocomplexity is a unique feature of Bristol Bay sockeye salmon, or if this concept applies to other salmon fisheries throughout the state. We addressed the question: do the characteristics of biocomplexity exist in Kuskokwim River sockeye salmon? Because the Kuskokwim is a large, dynamic river system rather than a series of glacially-carved lakes as in Bristol Bay, we did not necessarily expect that Kuskokwim sockeye would be structured similar to Bristol Bay. Indeed, in the Holitna River, river-type sockeye salmon show limited morphological, age, and size diversity. However, in Telaquana Lake, we found complexity in morphology, age, and size of sockeye salmon on par with the level of diversity found in Bristol Bay. These two systems differ in the types of spawning habitats available: the Holitna is comprised largely of riverine habitat, while riverine, beach, and inlet creek spawning habitat is found at Telaquana Lake. The findings of our study predict that returns to Telaquana should be more stable (at the drainage rather than individual spawning population level) than returns to the Holitna River, which are expected to show greater fluctuations from year to year. However, over longer time scales, such as glacial/inter-glacial (10,000 year) scales, the river-type sockeye salmon of the Holitna River should be more important for persistence of sockeye salmon in the Kuskokwim, because river-type sockeye tend to be more genetically diverse and show enhanced ability to re-populate newly available habitats.

XIII. APPENDICES:

Appendix A. Loadings for canonical variates 1-3 by landmark coordinate.

Landmark	Coordinate	CV1	CV2	CV3
1	X	103.609	38.432	19.371
	Y	10.858	-2.208	-9.584
2	X	-27.294	8.729	59.680
	Y	-123.254	63.531	-43.002
3	X	-97.894	-88.503	-63.460
	Y	189.532	106.387	43.654
4	X	75.298	-3.230	-6.667
	Y	-93.091	26.963	8.565
5	X	-43.149	32.688	1.293
	Y	94.224	-33.650	28.994
6	X	16.467	16.350	-54.562
	Y	-81.115	-37.525	-160.358
7	X	-6.391	121.649	95.558
	Y	34.887	-71.190	82.608
8	X	31.931	-9.448	32.281
	Y	53.797	100.294	126.578
9	X	-53.775	3.913	-99.475
	Y	13.484	-59.403	-93.920
10	X	18.443	-22.793	-25.713
	Y	-30.053	84.517	-5.704
11	X	-0.571	-118.259	4.775
	Y	-65.923	27.156	62.574
12	X	-27.309	-14.184	69.640
	Y	6.690	-11.638	-192.621
13	X	32.930	16.410	6.938
	Y	-25.927	-10.179	120.235
14	X	49.703	23.006	46.902
	Y	-32.703	-68.749	-29.576
15	X	-3.512	-8.459	0.348
	Y	-26.502	-6.981	40.366
16	X	-295.155	70.247	198.308
	Y	-200.421	178.592	-32.442
17	X	226.669	-66.550	-285.217
	Y	275.517	-285.918	53.634

Appendix B. Loadings for principle components 1-3 by landmark coordinate.

Landmark	Coefficient	PC1	PC2	PC3
1	X	0.130478	0.136659	-0.835908
	Y	0.051241	0.343995	0.044061
2	X	-0.014814	0.086933	0.026474
	Y	0.031038	0.130695	0.060629
3	X	0.113113	0.040584	0.178737
	Y	0.000898	-0.02328	-0.065255
4	X	-0.444777	0.337199	0.11653
	Y	-0.508716	0.110917	-0.061618
5	X	0.014318	-0.057027	0.185138
	Y	-0.345001	-0.073938	-0.07488
6	X	-0.007765	-0.039271	0.126522
	Y	-0.295651	-0.117321	-0.141132
7	X	-0.064584	-0.133524	-0.123842
	Y	-0.058003	0.042417	-0.020622
8	X	-0.043183	-0.094015	-0.073896
	Y	0.061554	0.14285	0.011268
9	X	-0.009313	-0.171303	-0.109815
	Y	0.162022	0.292986	0.074098
10	X	0.195089	0.064918	-0.000192
	Y	0.175586	0.23178	0.100506
11	X	0.164361	0.050326	0.021116
	Y	0.030519	-0.003246	0.030016
12	X	0.157832	0.101821	0.001267
	Y	-0.041532	-0.232191	-0.069016
13	X	0.033693	-0.000048	-0.084687
	Y	0.057858	-0.538156	0.001845
14	X	-0.103104	-0.080906	0.048663
	Y	0.137523	-0.263142	0.041613
15	X	-0.089112	-0.152336	0.226995
	Y	0.173187	-0.065222	0.007126
16	X	-0.018264	-0.054281	0.175226
	Y	0.179033	0.012944	0.04052
17	X	-0.013966	-0.035728	0.121671
	Y	0.188446	0.007912	0.020843

Appendix C. Allele frequencies, sample size, F_{IS}, and P-values for tests for deviation from Hardy-Weinberg expected proportions, by locus and locality. P-values in bold were considered statistically significant following adjustment for multiple tests.

Oki1a	*114*	*118*	*122*	N	F_{IS}	P
PCR	0.839	0.155	0.006	87	-0.094	0.722
BCR	0.868	0.132	--	91	0.142	0.173
UPB	0.903	0.097	--	93	0.390	**0.004**
SWB	0.920	0.074	0.005	94	0.069	0.448
OUT	0.832	0.142	0.026	95	-0.056	0.628
KOG	0.750	0.250	--	62	-0.067	0.741
CHU	0.714	0.286	--	42	0.195	0.264
HOL	0.739	0.261	--	71	0.166	0.215

Oki1b	*139*	*149*	*157*	*161*	N	F_{IS}	P
PCR	--	0.762	0.203	0.035	86	0.081	0.695
BCR	--	0.758	0.176	0.066	91	0.132	0.254
UPB	--	0.769	0.226	0.005	93	-0.046	0.820
SWB	--	0.814	0.176	0.011	94	0.277	0.013
OUT	--	0.684	0.184	0.132	95	0.042	0.169
KOG	--	0.613	0.379	0.008	62	-0.066	0.865
CHU	0.012	0.429	0.548	0.012	42	-0.234	0.130
HOL	--	0.647	0.346	0.007	68	0.052	0.861

One102	*203*	*207*	*211*	*215*	*219*	*223*	*227*	*231*	*235*	*239*
PCR	0.006	0.279	0.076	--	0.029	0.035	0.070	0.169	0.145	0.058
BCR	--	0.236	0.082	0.005	--	0.038	0.132	0.126	0.170	0.071
UPB	0.005	0.220	0.070	--	0.005	0.048	0.145	0.102	0.151	0.097
SWB	0.005	0.326	0.027	--	0.022	0.022	0.196	0.114	0.114	0.065
OUT	--	0.180	0.022	--	--	0.157	0.090	0.242	0.230	0.056
KOG	--	0.218	0.105	--	0.008	0.008	0.016	0.242	0.274	0.065
CHU	--	0.114	0.125	--	--	--	0.034	0.216	0.330	0.114
HOL	--	0.140	0.147	--	--	--	0.037	0.184	0.331	0.059

One102 (cont.)	*243*	*247*	*251*	*255*	N	F_{IS}	P
PCR	0.099	0.029	0.006	--	86	0.112	< **0.001**
BCR	0.099	0.016	0.022	--	91	0.006	0.296
UPB	0.102	0.027	0.027	--	93	0.015	0.624
SWB	0.065	0.043	--	--	92	0.035	0.176
OUT	0.006	0.017	--	--	89	0.032	0.959
KOG	0.040	0.008	0.008	0.008	62	-0.058	0.819
CHU	0.023	--	0.045	--	44	-0.069	0.498
HOL	0.066	--	0.007	0.029	68	0.186	< **0.001**

One105	*122*	*124*	*128*	*132*	*134*	*136*	*138*	*142*	*152*	N	Fis	P
PCR	--	--	0.891	0.109	--	--	--	--	--	87	0.001	1.000
BCR	--	--	0.890	0.110	--	--	--	--	--	91	0.331	0.010
UPB	--	--	0.830	0.160	--	0.011	--	--	--	94	0.001	0.379
SWB	0.011	--	0.867	0.096	--	0.021	--	--	0.005	94	-0.021	0.036
OUT	0.005	--	0.847	0.126	0.005	--	0.005	0.011	--	95	0.015	0.071
KOG	--	--	0.798	0.161	--	0.024	--	--	0.016	62	-0.193	0.486
CHU	--	0.012	0.744	0.232	--	0.012	--	--	--	41	-0.168	0.658
HOL	--	--	0.687	0.299	--	0.015	--	--	--	67	0.056	0.014

One108	*181*	*185*	*189*	*193*	*197*	*201*	*205*	*209*	*213*	*217*
PCR	0.065	0.018	0.276	0.376	0.076	0.041	0.012	0.006	0.024	--
BCR	0.027	0.049	0.209	0.385	0.049	0.060	0.005	0.005	0.055	0.038
UPB	0.016	0.069	0.213	0.346	0.165	0.080	--	--	0.005	0.011
SWB	0.011	0.037	0.266	0.351	0.096	0.074	0.032	--	0.011	0.005
OUT	--	0.089	0.458	0.174	0.026	0.089	0.026	--	--	0.053
KOG	--	0.008	0.137	0.315	0.113	0.194	0.024	0.040	0.024	0.081
CHU	--	0.048	0.214	0.131	0.190	0.083	0.083	0.071	0.024	0.107
HOL	--	0.031	0.162	0.254	0.169	0.069	0.015	0.062	0.069	0.123

One108 (cont.)	*221*	*225*	*229*	*233*	*237*	*241*	*245*	N	F_{IS}	P
PCR	0.018	0.006	--	0.006	0.018	0.018	0.041	85	0.146	0.088
BCR	0.066	0.005	0.005	--	0.011	0.011	0.016	91	0.031	0.261
UPB	0.048	0.021	0.005	0.005	--	0.011	0.005	94	0.094	0.205
SWB	0.048	0.021	0.005	--	0.016	0.016	0.011	94	0.057	0.835
OUT	0.068	--	--	--	--	0.016	--	95	0.117	0.090
KOG	0.008	0.008	0.016	0.032	--	--	--	62	-0.111	0.087
CHU	--	--	0.024	0.024	--	--	--	42	-0.033	0.890
HOL	0.031	--	0.008	0.008	--	--	--	65	0.247	< **0.001**

Ots100	*147*	*151*	*155*	*159*	*163*	*167*	*169*	*171*	*175*	*177*
PCR	--	0.012	--	--	0.564	0.366	--	0.017	--	--
BCR	--	0.005	--	0.022	0.604	0.352	--	0.011	--	--
UPB	--	--	--	0.043	0.553	0.309	--	0.032	--	--
SWB	--	--	--	0.011	0.468	0.383	--	0.032	--	--
OUT	--	--	--	0.011	0.543	0.223	0.005	0.016	--	--
KOG	--	--	0.008	--	0.040	0.460	0.194	0.048	0.016	--
CHU	--	--	0.011	0.011	0.136	0.386	0.114	0.091	--	0.023
HOL	0.016	--	--	--	0.095	0.397	0.095	0.079	0.008	0.008

Ots100 (cont.)	*183*	*185*	*187*	*191*	*195*	*201*	N	F_{IS}	P
PCR	--	--	0.017	--	0.023	--	86	0.112	0.011
BCR	--	--	0.005	--	--	--	91	0.101	0.555
UPB	--	0.005	0.005	0.016	0.032	0.005	94	0.003	0.029
SWB	--	--	0.027	0.043	0.037	--	94	0.025	0.173
OUT	--	0.005	0.016	0.016	0.163	--	92	0.191	0.026
KOG	0.089	0.056	--	0.089	--	--	62	0.166	0.021
CHU	0.068	0.080	--	0.057	0.011	0.011	44	-0.017	0.467
HOL	0.063	0.063	0.016	0.143	--	0.016	63	0.243	< **0.001**

Ots107	*106*	*110*	*114*	*118*	*122*	*126*	*130*	N	F_{IS}	P
PCR	--	0.017	0.580	0.121	0.011	0.230	0.040	87	-0.001	0.754
BCR	--	0.005	0.582	0.176	0.005	0.209	0.022	91	0.011	0.584
UPB	--	0.005	0.601	0.165	0.016	0.197	0.016	94	-0.017	0.031
SWB	--	0.005	0.606	0.128	--	0.197	0.064	94	-0.164	0.287
OUT	0.005	--	0.721	0.037	0.005	0.232	--	95	-0.035	0.295
KOG	--	0.148	0.779	0.033	--	0.041	--	61	-0.013	0.785
CHU	--	0.048	0.905	0.024	--	0.024	--	42	0.209	0.148
HOL	--	0.062	0.896	0.042	--	--	--	72	0.066	0.347

One109	*123*	*127*	*131*	*143*	*147*	*151*	*155*	*159*	*163*	*167*
PCR	--	0.040	--	0.029	0.057	0.080	0.121	0.483	0.115	0.063
BCR	0.016	0.027	--	0.016	0.022	0.093	0.126	0.516	0.110	0.066
UPB	0.005	0.027	--	0.021	0.048	0.090	0.090	0.505	0.106	0.090
SWB	0.021	0.032	--	0.037	0.064	0.133	0.069	0.404	0.197	0.043
OUT	0.011	0.011	--	0.063	0.026	0.005	0.042	0.726	0.084	0.032
KOG	0.202	0.282	0.016	0.032	0.048	0.089	0.024	0.105	0.073	0.073
CHU	0.134	0.293	0.037	0.037	0.098	0.085	0.037	0.122	0.085	0.037
HOL	0.169	0.218	0.014	0.007	0.042	0.162	0.028	0.183	0.042	0.085

One109 (cont.)	*171*	*175*	*183*	N	F_{IS}	P
PCR	0.011	--	--	87	0.020	0.316
BCR	0.005	--	--	91	0.098	0.319
UPB	0.005	--	0.011	94	0.040	0.048
SWB	--	--	--	94	0.090	0.019
OUT	--	--	--	95	0.108	0.497
KOG	0.032	0.024	--	62	0.110	0.014
CHU	0.024	0.012	--	41	0.095	0.093
HOL	0.014	0.035	--	71	0.179	0.186

One111	*192*	*196*	*200*	*204*	*208*	*212*	*216*	*220*	*224*	*228*
PCR	0.037	0.194	0.131	0.150	--	--	0.006	--	--	--
BCR	0.055	0.143	0.077	0.132	0.005	--	--	--	--	--
UPB	0.011	0.102	0.113	0.108	0.005	--	--	--	--	--
SWB	--	0.133	0.138	0.122	--	--	0.005	--	--	--
OUT	--	0.379	0.232	0.205	0.005	--	--	--	--	--
KOG	--	--	0.336	0.303	0.057	0.033	--	--	--	0.008
CHU	--	0.012	0.256	0.402	0.073	0.061	--	--	0.012	--
HOL	--	--	0.289	0.387	0.070	0.007	--	0.014	--	--

One111 (cont.)	*232*	*236*	*240*	*244*	*248*	*252*	*256*	*264*	*268*	*280*
PCR	--	--	0.006	0.019	0.006	--	--	--	0.006	--
BCR	--	--	0.027	0.016	0.060	--	--	--	0.011	--
UPB	--	0.005	0.011	0.022	0.054	0.011	--	0.005	--	--
SWB	0.005	0.005	0.021	0.027	--	0.005	--	--	0.005	--
OUT	--	--	0.016	0.005	--	--	0.016	--	--	--
KOG	0.025	0.008	0.008	0.016	0.041	--	--	--	--	0.016
CHU	--	--	0.012	0.024	0.024	--	--	--	--	0.012
HOL	0.028	0.014	0.007	0.007	0.028	--	--	--	--	--

One111 (cont.)	*284*	*288*	*292*	*296*	*300*	*304*	*308*	*312*	*316*	*320*
PCR	--	0.019	0.037	0.006	0.062	0.062	0.075	0.100	0.081	--
BCR	--	0.005	0.033	0.022	0.159	0.027	0.066	0.082	0.044	0.027
UPB	--	--	0.016	0.022	0.086	0.038	0.129	0.129	0.113	0.022
SWB	--	0.011	0.011	0.016	0.043	0.090	0.144	0.112	0.080	0.027
OUT	--	--	0.047	0.011	--	0.026	0.037	0.021	--	--
KOG	0.008	--	0.033	0.057	0.025	0.016	0.008	--	--	--
CHU	--	0.012	0.012	0.049	0.024	0.012	--	--	--	--
HOL	0.007	0.014	0.028	0.056	0.028	0.014	--	--	--	--

One111 (cont.)	*328*	N	F_{IS}	P
PCR	--	80	0.078	0.100
BCR	0.005	91	0.072	0.373
UPB	--	93	0.115	0.032
SWB	--	94	0.068	0.054
OUT	--	95	0.113	0.082
KOG	--	61	0.065	0.536
CHU	--	41	0.079	0.305
HOL	--	71	0.223	**0.004**

One14	*131*	*133*	*135*	*137*	*139*	*141*	*143*	*145*	*147*	*149*
PCR	--	0.024	0.458	--	0.012	0.012	0.006	0.452	--	0.036
BCR	--	0.017	0.400	--	0.017	--	--	0.511	--	0.056
UPB	--	0.005	0.330	--	0.005	0.005	--	0.599	--	0.055
SWB	0.016	0.005	0.484	--	0.021	0.005	--	0.431	--	0.037
OUT	0.005	--	0.533	--	--	--	--	0.462	--	--
KOG	--	0.032	0.097	0.008	--	--	--	0.831	0.032	--
CHU	--	0.073	0.061	0.012	0.012	--	--	0.780	0.037	0.012
HOL	--	0.014	0.043	--	0.007	--	--	0.864	0.029	0.014

One14 (cont.)	*153*	*154*	*157*	*183*	N	F_{IS}	P
PCR	--	--	--	--	83	-0.005	1.000
BCR	--	--	--	--	90	0.078	0.507
UPB	--	--	--	--	91	0.258	**0.001**
SWB	--	--	--	--	94	0.103	**0.009**
OUT	--	--	--	--	91	0.153	0.143
KOG	--	--	--	--	62	-0.019	0.299
CHU	--	0.012	--	--	41	-0.144	1.000
HOL	0.007	--	0.007	0.014	70	0.377	0.012

One18	*169*	*171*	*173*	*175*	*179*	*183*	*201*	*209*	N	F_{IS}	P
PCR	0.881	0.030	0.048	--	0.006	0.036	--	--	84	0.030	0.489
BCR	0.912	0.027	0.027	--	0.005	0.027	--	--	91	-0.055	1.000
UPB	0.910	0.011	0.027	--	--	0.053	--	--	94	0.061	0.403
SWB	0.935	0.016	0.016	--	--	0.032	--	--	93	-0.041	1.000
OUT	0.884	0.042	--	0.011	0.021	0.042	--	--	95	-0.077	1.000
KOG	0.605	--	--	--	0.177	0.218	--	--	62	0.137	0.052
CHU	0.488	--	--	--	0.183	0.329	--	--	41	0.147	0.102
HOL	0.514	--	--	--	0.239	0.232	0.007	0.007	71	0.037	0.025

One8	*193*	*195*	*199*	*201*	*203*	*205*	*207*	*209*	N	F_{IS}	P
PCR	0.018	--	--	0.982	--	--	--	--	85	-0.012	1.000
BCR	0.013	--	0.006	0.968	--	0.006	0.006	--	78	-0.015	1.000
UPB	0.027	--	0.022	0.946	--	0.005	--	--	93	-0.034	1.000
SWB	0.027	--	0.022	0.935	--	0.016	--	--	93	-0.040	1.000
OUT	0.013	--	0.013	0.975	--	--	--	--	80	-0.013	1.000
KOG	0.069	0.034	0.414	0.405	0.060	0.017	--	--	58	0.113	0.027
CHU	0.024	0.061	0.354	0.500	0.024	0.012	--	0.024	41	0.380	**0.001**
HOL	0.101	0.029	0.290	0.522	0.022	0.014	--	0.022	69	0.364	**<0.001**

Str60	*117*	*119*	*127*	*129*	*133*	N	F_{IS}	P
PCR	0.346	0.006	0.006	0.583	0.058	78	0.051	0.218
BCR	0.429	0.006	0.045	0.494	0.026	77	0.118	0.336
UPB	0.190	--	0.065	0.667	0.077	84	-0.070	0.401
SWB	0.259	--	0.029	0.684	0.029	87	0.138	0.415
OUT	0.066	--	--	0.898	0.036	83	-0.080	1.000
KOG	0.508	0.175	--	0.300	0.017	60	0.122	0.678
CHU	0.568	0.162	--	0.257	0.014	37	-0.094	0.926
HOL	0.463	0.125	--	0.397	0.015	68	-0.026	0.328

One21	*246*	*250*	N	F_{IS}	P
PCR	0.962	0.038	78	-0.034	1.000
BCR	0.954	0.046	76	-0.042	1.000
UPB	0.975	0.025	81	-0.019	1.000
SWB	0.978	0.022	89	-0.017	1.000
OUT	0.988	0.012	83	-0.006	1.000
KOG	1.000	--	60	--	--
CHU	1.000	--	38	--	--
HOL	0.992	0.008	66	--	--